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PROTEIN AND ENERGY IN RATIONS
FOR FATTENING HOLSTEIN STEERS

by



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A THESIS

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OF MASTER OF SCIENCE

DEPARTMENT OF ANIMAL SCIENCE

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Protein and Energy in Rations for Fattening Holstein Steers" submitted by Ross Rawling Moon, B.Sc. (Ag.), in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

Twenty-seven Holstein steers were fed high-barley diets at three levels of crude protein (8.7, 11.9, and 14.2 percent) and three levels of energy (ad libitum, 88.5, and 79.8 percent of ad libitum) in an attempt to establish optimum dietary levels of crude protein and gross energy. Crude protein increments were achieved by substitution of soybean meal for barley, and gross energy increments were achieved by feed restriction. Average initial and final liveweights were 319 and 413 kg., respectively. Metabolism studies were conducted midway through the trial.

Average daily gains obtained were 0.70, 0.78, and 0.78 kg., respectively for the low, medium, and high protein groups, and 0.91, 0.74, and 0.61 kg., respectively, for the high, medium, and low energy groups. Daily gain was affected ($P < 0.01$) by the level of energy fed. A multiple regression equation was developed from the data, which described a saddle-shaped response surface. A simple nutrient-cost study was attempted to illustrate the relative degrees to which protein and energy might be substituted for each other.

The gain data indicated a reduced benefit obtained by supplying increased energy beyond the medium level when protein was at a low level. At high protein intakes, it appeared that there was quite an accelerated need for dietary energy. When energy was restricted, there was no advantage to supplying more protein than beyond the medium protein level. At the high energy level, there was no benefit from supplying any more crude protein than at the medium protein level. It appeared that the crude protein to gross energy ratio of 32.0 g. per Mcal was optimal for the energy levels used in this study.

The efficiency of utilization of dry matter and gross energy for liveweight gain was highest at the high protein level (8.0 kg./kg.; 34.6 Mcal/kg., respectively), and the efficiency of utilization of crude protein for liveweight gain

was highest at the low protein level (0.89 kg./kg.). The efficiency of utilization of dry matter, crude protein, and gross energy for liveweight gain was highest at the high energy level (7.7 kg./kg.; 1.02 kg./kg.; 33.3 Mcal/kg., respectively). Some isoquants for efficiency of utilization of crude protein for liveweight gain were examined.

Estimates of carcass fat, such as separable fat of the tenth rib, ether extract of the separable rib lean, kidney fat weight, and backfat thickness all tended to display lowest amounts or percentages at the medium protein level, and highest amounts or percentages at the medium energy level. Ether extract in the lean, amount of marbling, and Mcal of gross energy incorporated per kilogram of liveweight gain were all lowest at the high energy level.

The superiority of the medium protein-high energy treatment may be a combination of trends toward least carcass fat at the medium protein level, and least intramuscular fat at the high energy level. The steers receiving the medium protein-high energy combination, with the protein:energy ratio of 32.0, displayed the least requirement of dry matter and gross energy per kilogram of gain, were on feed the shortest length of time, and had superior gains.

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TABLE OF CONTENTS

	Page
INTRODUCTION	1
REVIEW OF LITERATURE	3
Energy – as a nutrient and a basis for ration formulation	3
Protein – its place as a nutrient	5
Protein—Energy Interactions	8
Protein and Energy Levels	11
Protein:Energy Ratios	16
Considerations with Respect to Ruminants	18
EXPERIMENTS AT THE UNIVERSITY OF ALBERTA	22
Introduction	22
Experimental	22
Design	22
Animals and Management	22
Experimental Rations	23
Energy Restriction	24
Metabolism Studies	24
Carcass Measurements	26
Analytical Methods	27
Statistical Analyses	27
RESULTS AND DISCUSSION	29
Protein and Energy Intake	29
Average Daily Gain	29
Efficiency of Utilization of Dry Matter, Crude Protein, and Gross Energy for Weight Gain	39
Coefficients of Apparent Digestibility	45

TABLE OF CONTENTS

	Page
Urinary Crude Protein and Gross Energy Outputs and Retentions	50
Viscera Abnormalities	52
Kidney Fat, Backfat Thickness, and Marbling	54
Dressing Percentage, Rib-Eye Area, Cutability, and Grade . .	57
Physical Analysis of Rib Samples	61
Chemical Analyses of Rib Samples	64
SUMMARY	69
BIBLIOGRAPHY	72
APPENDIX	i

LIST OF TABLES

	Page
Table 1. Ration formulations and analysis	25
Table 2. Intake of dietary crude protein and gross energy	30
Table 3. Average daily weight gain	31
Table 4. Average initial and final liveweights and days on feed	40
Table 5. Dry matter intake and efficiencies of feed utilization	42
Table 6. Comparison of the efficiency of utilization of dietary energy for liveweight gain among various weight classes of animals . .	46
Table 7. Coefficients of apparent digestibility	47
Table 8. Urinary crude protein and gross energy outputs and retentions .	51
Table 9. Kidney fat, backfat thickness, and marbling	55
Table 10. Dressing percentage, rib-eye area, and cutability	58
Table 11. Separable lean, fat, and bone of the tenth rib	62
Table 12. Chemical analysis of the tenth rib	65
Table 13. Comparison of carcass characteristics of two weight-groups of Holstein males	68
Appendix Table A. The derivation of isoquants	i
Appendix Table B. Mean squares obtained by analysis of variance	ii

LIST OF FIGURES

	Page
Figure 1. Nitrogen balance as related to caloric and protein intake	9
Figure 2. Daily protein and energy intake in relation to maintenance and weight gain	12
Figure 3. The effect of dietary crude protein and gross energy on average daily gain	33
Figure 4. Gain isoquants for crude protein and gross energy inputs per metabolic weight	38
Figure 5. Crude protein per gain isoquants for daily crude protein and gross energy inputs	44

INTRODUCTION

It has been recognized for many years that nutrient ratios may have as much, or even more importance than actual nutrient levels. The dietary ratio of protein to energy may be classified as the most important of these ratios. Protein and energy together represent the bulk of the total nutrient cost of any ration, and therefore intake levels of each of these nutrients are of prime importance.

Protein requirements of an animal for a certain rate of gain are dependent on the level of energy to be supplied, and energy requirements are in the same way dependent on the protein level fed. Several combinations of protein and energy may support a given rate of gain, and hence the specific combination used will be dependent on the relative costs of protein and energy, and the effect that these levels of protein and energy may have on carcass composition.

The optimum protein:energy ratio for liveweight gains in ruminants should be dependent on the age and stage of growth of the animal, and may be influenced by such factors as breed, disease, climatic conditions, or other stresses. Strictly speaking, in ruminants, the diet must contain a ratio of protein:energy that is optimum for the rumen microorganisms, as under normal feeding practices, microbial digestion of food in the rumen determines to a large extent the protein and energy available to the host animal.

Much of the present knowledge of nutrient requirements has been determined with early-maturing and early-fattening British beef breeds. In recent years it has been recognized that larger, later-maturing breeds, such as the Holstein, that have a longer period of growth, may offer a very substantial contribution to beef production. Optimum nutrient ratios for these breeds may be different from those incorporated into current feeding standards. The use of very high levels of grain in rations for intensive beef production may also influence nutrient ratios required.

Consequently, this study was carried out with 319-kg. Holstein steers,

to examine the effects of three protein:energy ratios on daily gain, daily feed consumption, feed efficiency, digestibility of the rations, and carcass quality and composition.

REVIEW OF LITERATURE

Energy - as a nutrient and a basis for ration formulation

It has long been recognized that the animal body has a requirement for dietary energy. If there is no supply of energy given in the diet, the animal must eventually use its own body tissues as a source to provide energy for the "life functions" such as muscular activity, tissue synthesis, and chemical energy used in active transport.

Energy as a nutrient is so important to the animal that it is the factor which dictates consumption, at least in the case of monogastrics (Hill and Dansky, 1954; Crampton, 1965). It is also thought that ruminants eat to meet a specific energy requirement (Kennedy, 1961), but this is complicated by many other factors, such as dry matter content of the feed, rumen size, food particle size, and the rate of passage through the rumen.

Gordon and Forbes (1970), using lactating cows as test animals, found that the level of dietary energy significantly affected body weight change. Animals fed only 80 percent of their estimated energy requirements lost weight, while those fed 120 percent of their estimated energy requirements gained weight. Also, the higher level of energy was associated with a higher digestibility of the organic matter in the total diet. Increasing the dietary energy also had the effect of decreasing nitrogen digestibility and increasing nitrogen retention. These results are in agreement with those of Broster et al. (1969). Shaw (1961), Nicholson et al. (1962a, 1962b), Rook et al. (1963), Broster et al. (1965), and Burt (1966) all obtained data showing increases in either nitrogen balance or liveweight gain from additional energy.

Andrews and Ørskov (1970b) found a significant linear decrease in the ether extract content, and a corresponding linear increase in nitrogen content of

40-kilogram lamb carcasses with increased level of feeding.

Inasmuch as animals eat to meet a calorie requirement, then it would seem feasible and sensible that the requirements for other nutrients be expressed in terms of the energy requirement. The basis of Henry's "nutritive ratio", coined by him in 1904, (cited by Crampton, 1964) was the proportion of protein to carbohydrate equivalent. This was one of the first attempts to consider rations in terms of their energy content. Guilbert and Loosli, in their classical paper in 1951, computed for farm animals the recommended digestible crude protein (DCP), calcium, phosphorus, carotene, vitamin A, vitamin D, thiamine, riboflavin, niacin, and pantothenic acid per unit of total digestible nutrients (TDN) for individuals at body weights of from ten percent to 100 percent of expected adult size. In their study, they suggested that the feasibility of expressing the relationship of the various nutrients with metabolizable energy (ME) rather than with TDN should be explored. Stare (1958) also considered calories in his definition of a balanced ration, which he said was "... the type of nutrition that supplies a sufficiency, but not an excess, of calories coming from both carbohydrates and fat ... in adequate ratio with vitamins, minerals, and amino acids." Johnston (1958) also advocated a calorie basis for expressing nutrients such as protein. He thought it preferable not to speak of the amount of protein per kilogram daily, but to express it as the percentage of calorie intake.

Crampton (1965) put forth a very strong and a very logical argument for basing all nutrient requirements on energy. He stated, "To the extent that degrees of metabolic activity (physical and/or productive) are directly reflected in the caloric intake necessary to maintain energy equilibrium, it follows that the nutrient needs are directly or indirectly related to and hence logically expressed in ratio to energy needs." Kleiber (1961) put forth the argument that not only the requirements of food energy, but also that of protein and of most vitamins may be expressed per

unit of the three-quarter power of body weight ($W_{kg}^{0.75}$), because these dietary requirements are directly related to energy metabolism.

Present nutritional standards are based on a weight basis-- either daily, or per unit of feed. Thus, there is no consideration given to the plane of energy which the animal might receive. As can be seen from the above discussion, this might have an important bearing on the nutritional needs of the animal. For example, the levels of vitamins and minerals that are needed to metabolize energy are also dependent on energy intake, rather than on the amounts of the ration (Crampton, 1965). Hence, in the words of Crampton (1965), "there is sound biological thinking behind the thesis that energy, rather than feed intake, should be the dietary component relative to which nutrient needs are adjusted." When growing mammals are compared on the basis of the percent of the adult weight attained, as was done by Guilbert and Loosli (1951), the protein-energy ratios of their requirements are probably the same, and fit into a common pattern of declining protein needs relative to energy as they near adult weight.

Another strong argument for the use of energy as a basis for ration formulation is the fact that it does not seem to differ with species. Putting digestible crude protein (DCP) requirements of adult ruminants and adult swine on the basis of DCP / 1000 kcal. of ME, Crampton (1965) found that the requirements were independent of body weight and fairly constant at approximately 25 g. Hence, this would definitely indicate a metabolic basis for nutrient requirements with respect to energy.

Protein - its place as a nutrient

Along with energy, protein is one of the most important animal nutrients required. Its importance may be demonstrated by the fact that if an animal's diet is low in protein, it will not be readily consumed (Campling et al., 1962; Elliott and Topps, 1963). It has been recognized for many years that dietary protein is

used in the animal body for the essential function of building body proteins. Protein is also important in the animal body as an energy source.

The effects of varying dietary protein in rations for various classes of livestock have been well documented. Jones and Hogue (1960) found with fattening lambs that the animals receiving a high level of protein (120 percent of the minimal requirements according to Morrison's (1957) standard) gained faster, graded better, and were more efficient than those fed at a low level (90 percent of Morrison's (1957) standard). Raleigh (1970) reported that digestible protein was usually the first nutrient limiting production in beef cattle on pasture, and consequently supplemented yearling steers on fall pasture according to their protein needs. Broster et al. (1969) reported a number of experiments done on dairy heifers in which protein levels were varied. They found that increasing crude protein in isocaloric diets was beneficial in increasing rate of gain in two-year-old non-pregnant heifers, but only up to a certain level. In another experiment on two-year-old barren heifers, they found that additional protein increased the digestibility of protein in the ration. Putnam et al. (1966) reported the same effect using beef heifers. In a trial with yearling steers, Broster et al. (1969) reported that the addition of protein to the diet increased the digestibility of the fibre. This may be in accordance with Campling et al. (1962), who found that the addition of urea intraruminally led to increased consumption in cows fed oat straw (about three percent crude protein). Elliott and Topps (1964) found that the digestibility of low protein diets (four percent crude protein) and their intake by sheep were appreciably lower than corresponding values obtained for the diets higher in protein.

Elliott et al. (1964), working with African cattle found that liveweight gain was significantly increased by increases in the level of digestible crude protein. Kliwer et al. (1970) found that increasing the dietary crude protein level from 11 to 15 percent improved average daily gains and feed conversion in growing Holstein

steers, but reduced dressing percentage and rib-eye area, and increased back-fat thickness. Using isocaloric rations with three protein levels (11, 14 or 17 percent crude protein), Kay et al. (1967) found that up to 200 kilograms liveweight, mean growth rate and feed conversion efficiency for Holstein steers were significantly poorer for the low protein diet than for the medium and high diets. At greater weights, however, there were no significant differences between treatments in either growth or feed conversion efficiency. There was a suggestion that carcasses from steers given the high protein diet had a greater proportion of fat and a lower proportion of water than those from steers given the low protein diet, as measured by chemical analysis of the tenth rib. In some similar work done by Kay et al. (1968) with similar rations and animals, they found that the dry matter intake was lower for the steers given the 11 percent crude protein diet, and their liveweight gain was lower up to 250 kilograms. Beyond 250 kilograms, their gain was similar to that of the steers on the 14 and 17 percent crude protein treatments. They further found that both dry matter digestibility and apparent nitrogen digestibility were lowest for those steers given the diet containing 11 percent crude protein. Again, there was a trend toward a higher fat content and a lower water content in the tenth rib from steers given the high protein compared with those fed the low protein diet.

In trials with lactating dairy cows, Gordon and Forbes (1970) found that raising the level of dietary protein to 120 percent of the estimated requirement from 80 percent of the estimated requirement resulted in a significant improvement in the apparent digestibility of the nitrogen of the ration. Andrews and Ørskov (1970b) showed linear increases in the rate of deposition of protein and decreases in the fat deposition with increases in the concentration of crude protein fed to early-weaned lambs. Gardner (1968b) found that as the level of digestible crude protein fed to dairy calves was increased from five to 9.5 percent, the kilograms of DCP used per kilogram of gain increased from 0.29 to 0.45. Clanton and Zimmerman (1970) using

heifer calves on pasture reported that protein was the first-limiting nutrient, and that there was no benefit in supplying energy unless protein levels were first supplemented. Prés (1964) indicated, that with six-month-old Black Pied Lowland Cattle, the retention, utilization, and digestibility of nitrogen was higher with more protein in the ration. This worker found that the amount of dietary protein had little effect on digestible crude protein consumed per kilogram of weight gained. Stobo et al. (1967c) found that decreases in the crude protein content of the diet led to reductions in dry matter digestibility. This finding is also in agreement with the results of Brown et al. (1956), Brown et al. (1958), and Whitelaw et al. (1961). Zimmerman et al. (1961) reported increased gains from adding protein to the diet of ten-month-old Hereford-Angus steers.

Protein - Energy Interactions

From the above review of the status of protein and energy in animal nutrition, there have been a few indications of an interrelationship between protein and energy. Several authors have pointed out associative effects of protein and energy in the diet. Calloway and Spector (1954) did several experiments with human subjects to elucidate the effects of protein and calorie intake on nitrogen balance. They found that under normal nutritional conditions, nitrogen balance is improved by either an increase in energy intake or in protein intake. However, the beneficial effect of a rise in energy intake can be modified or prevented by an inadequate protein intake, and conversely, an increased protein intake may not be fully effective because of insufficient energy in the diet. Apart from these occasions, protein intake and energy intake appear to have independent effects on nitrogen balance. This relationship is evident as shown in Figure 1. The parallel slopes of the nitrogen retention lines show equal responses to additions of energy at a given protein level, and equal responses to additions of protein at a given

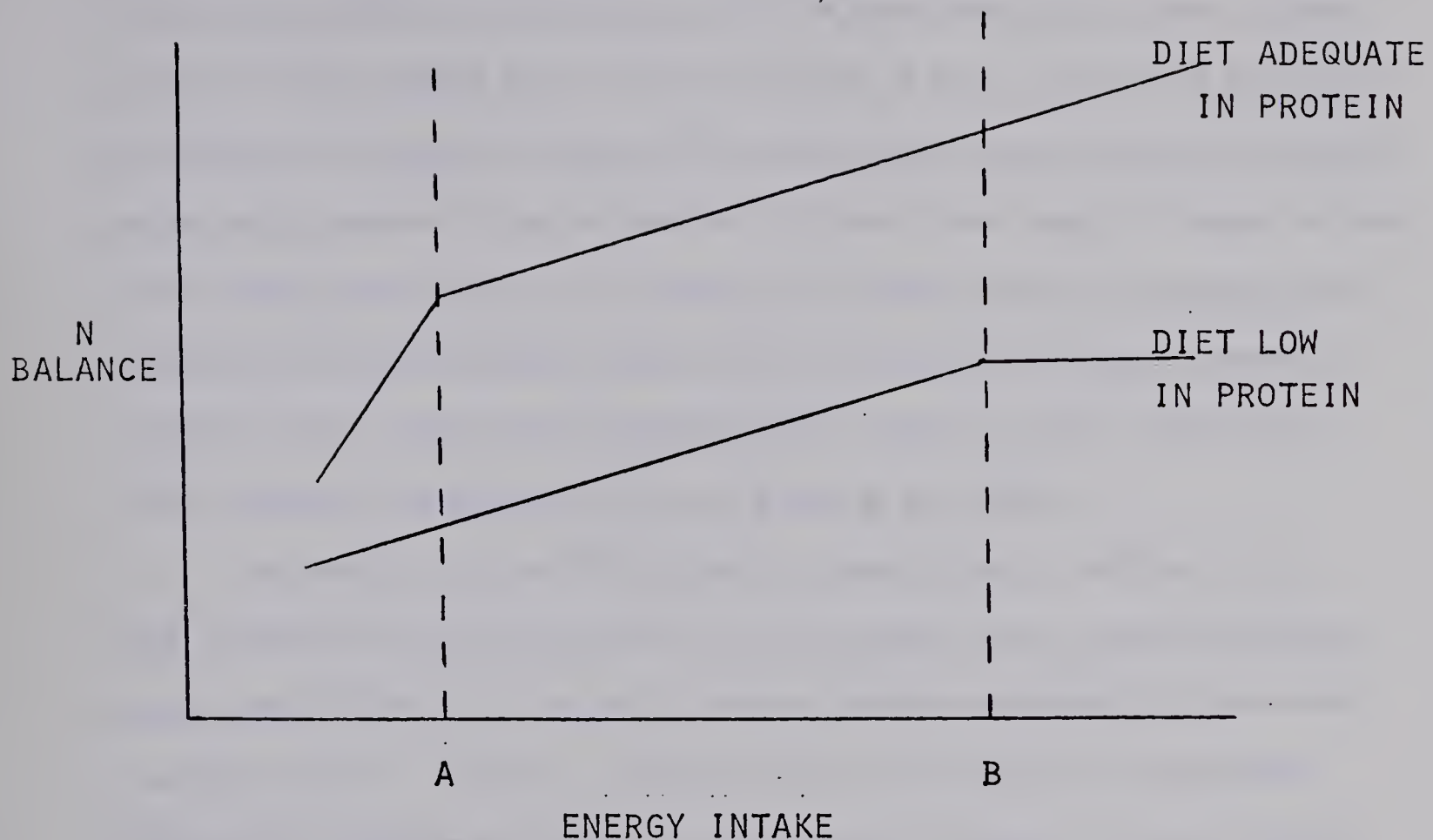


FIGURE 1. NITROGEN BALANCE AS RELATED TO CALORIC AND PROTEIN INTAKE (CALLOWAY AND SECTOR, 1954)

energy level. However, at energy levels below A there is not enough energy available to make use of the protein in a diet adequate in protein. At energy levels higher than B the lack of protein in the low protein diet becomes the limiting factor, and hence the additional energy supplied is of no benefit.

The relationship between nitrogen balance and energy has been demonstrated to exist in rats from sub-maintenance levels up to surfeit levels, providing that the level of protein intake is adequate (Munro and Naismith, 1953). In fact, the degree of nitrogen retention was found to be approximately proportional to the energy added. It may be noted here that both carbohydrate and fat appear to be equally effective as energy sources for the purpose of causing nitrogen retention.

Bowland et al. (1958) and Likuski et al. (1961) demonstrated similar trends. Blaxter and Wood (1951) reported that in the milk-fed calf, if equal quantities of gross energy are supplied, the storage of nitrogen falls as the protein content of the diet is reduced, and for equal amounts of nitrogen apparently digested, the storage of nitrogen increases with increasing energy intake. The response of nitrogen balance to increased protein intake has been demonstrated by Munro (1951); the response of nitrogen balance to increased caloric intake has been demonstrated by Swanson (1951), Lofgreen et al. (1951), Cailoway and Spector (1955), and Broster et al. (1969).

According to Munro (1964) vigorous nitrogen retention continues for at least 15 days after feeding large amounts of extra energy to man, and the additional energy was still effective in improving nitrogen retention when fed 5 1/2 hours after the dietary protein. However, in the case of man, the ingestion of carbohydrate and protein in the same meal results in a much greater increase in nitrogen retention as compared with their separate consumption. This is presumably due to an interaction between dietary carbohydrate and protein in the same meal, which is an action confined to carbohydrate and is distinct from its effect on protein metabolism as an energy source. This action is due to the induced secretion of insulin caused by the presence of the carbohydrate. The insulin, an anabolic hormone, induces deposition of protein in the body periphery. Hence it is mostly deposited in a non-labile state, although some is deposited in the form of labile muscle protein.

The characteristic feature of labile nitrogen retained as a result of adding protein to the diet is that it is all released again when protein intake is reduced to its former level. In contrast to this, very little of the quite large retention of nitrogen caused by increasing the energy content of an already adequate diet is lost again when caloric intake is diminished. Presumably, energy intake exerts a continuous influence on the utilization of circulating amino acids for all synthetic purposes, notably during the post-absorptive period. Labile protein deposition is only a small part of this utilization. Consequently, the nitrogen retention caused

by adding extra energy to the diet differs in its mechanism from the nitrogen retention induced by adding extra protein to the diet. Additional protein added to the diet of the well-fed adult animal seems to induce a nitrogen retention caused mainly by labile protein deposition.

Calloway and Spector (1954) concluded that: "on a fixed adequate protein intake, energy level is the deciding factor in nitrogen balance and that with a fixed adequate caloric intake, protein level is the determinant... with the corollary ... at each fixed inadequate protein intake there is an individual limiting energy level beyond which increasing calories without protein or protein without calories is without benefit." The truth of this conclusion is being continuously strengthened by increasing numbers of research reports.

Protein and Energy Levels

Protein and energy can be fed in many combinations of levels for a given class of livestock. This has been illustrated in Figure 2 by Winchester and Harvey (1966). It can be seen that there are an infinite number of combinations of protein and energy that could produce the desired weight gain, but only one is most economical of energy, that is the minimum point of each curve. Blaxter and Wood (1951), Brisson et al. (1957), Preston (1966), and Jacobson (1969) indicated that the protein: energy ratio does not remain constant, since the requirement for protein in relation to energy increases with increasing rate of gain. Brown et al. (1958) found that Holstein and Jersey calves gained weight at a faster rate when fed a concentrate mixture containing 16.2 percent crude protein than when the concentrate contained 8.5, 13.0, 20.0, or 23.7 percent crude protein. These workers thus postulated that the 16 percent crude protein concentrate gave a ratio of protein to energy that was optimal. Brown and Lassiter (1962) confirmed the existence of an optimal protein:energy ratio in the diet of the growing calf. Gordon and Forbes (1970) found an associative effect of

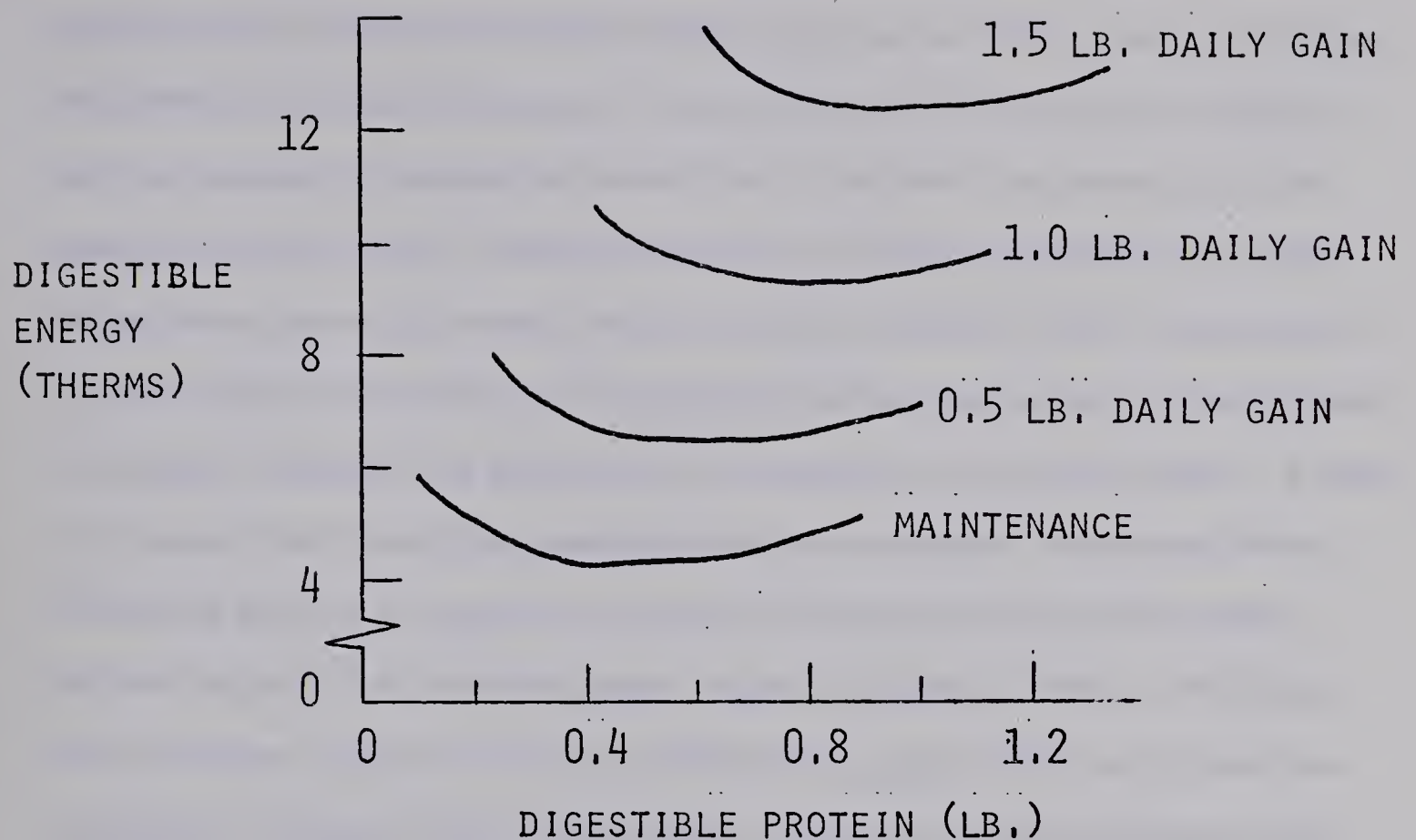


FIGURE 2. DAILY PROTEIN AND ENERGY INTAKE IN RELATION TO MAINTENANCE AND WEIGHT GAIN (WINCHESTER AND HARVEY, 1966)

energy and protein with respect to milk production in Shorthorn cows. They found that the milk yield at any level of energy intake, and the response in milk yield and composition to changes in energy intake, depended on the level of protein intake. Bowland and Berg (1959) found that pigs fed high energy-high protein rations throughout the feeding period had superior liveweight gains to those pigs fed lower protein and energy levels. Jones and Hogue (1960) detected a significant interaction between dietary protein and energy in average daily gain, liveweight grade, and feed efficiency of fattening lambs. The high protein - high energy groups gained faster and graded better than the other groups. However, the high protein - low energy group were the most efficient in terms of therms of energy required per

pound of gain. The low protein-high energy groups gained slower, were less efficient, and graded lower than other groups. Thus, as the level of energy was increased, it was also necessary to increase the protein level to maintain feed consumption and growth rate of the animals. Raleigh and Wallace (1962) confirmed the same trend, as they found that at high energy levels, low levels of protein intake limited growth of weaner calves very severely. Other researchers have also arrived at a low protein-high energy combination by adding additional energy to a low protein ration. It seems in all cases, that a lower than average response was obtained. Blaxter and Price (1946) used starch as a supplement to a basal low protein ration for dairy heifers, but found no benefit in liveweight gains. Harris and Mitchell (1941a, 1941b) used starch and sugar supplements for sheep and Fontenot et al. (1955) used glucose as a supplement for Hereford steers. Both groups of workers used these supplements with low protein rations (five to eight percent crude protein) but found no benefit in weight gain. Elliott et al. (1964) also found smaller than average gains in African cattle when additional energy was fed at very low protein intakes. The reason for these results was explained by two groups working independently in 1962. Wagle et al. (1962) found that a low protein intake limits the need for food energy by limiting growth. Munro et al. (1962) concluded that the failure of protein metabolism to respond to increased caloric intake on a protein-free diet is due to the limitation on the rate of protein synthesis imposed by such a diet.

However, it has been demonstrated that addition of energy to diets containing a higher level of protein allows the extra energy to be used. For example Mitchell et al. (1940) and Fontenot et al. (1955) reported that the addition of glucose to a basal ration of 12 percent crude protein for steers was beneficial. Blaxter and Wood (1951), Lofgreen et al. (1951), and Stobo et al. (1967a, 1967b) all obtained responses from additional energy in rations of 12 percent crude protein with young calves. Clanton et al. (1965), and Clanton and Zimmerman (1970), reported no advantage

in supplementing heifer calves with additional energy above 2.4 Mcal/day when the crude protein supplementation was held at 0.14 or 0.18 kg. of crude protein daily. There were significant gains with increased energy levels when the protein intake was elevated to 0.27 or 0.36 kg. of crude protein per day though, indicating that the higher protein levels allowed the extra energy to be beneficial.

There is little use in supplying adequate protein unless the energy level of the diet is high enough that use can be made of it. Broster et al. (1969) found in feeding two-year-old non-pregnant heifers that there was little response to additional protein above 1.71 lb. of crude protein per day when the energy level remained constant at 0.95 lb. of starch equivalent per day per 100 lb. of mean liveweight. In fact, the rate of gain was found to decrease at the highest crude protein intake of 2.90 lb. of crude protein per day. This is in agreement with results reported by Erwin et al. (1961) in which liveweight gain of yearling steers fell at high protein levels. Elliott et al. (1964) also found that at high protein-low energy, gains were depressed more than at medium protein-low energy. In experiments done with yearling heifers, Broster et al. (1969) found that increasing the dietary energy of the diet from 12.3 to 14.4 Mcal of crude metabolizable energy per day, at a constant crude protein intake of 1.5 lb. per day, resulted in a significant increase in liveweight gain. The response to additional energy seemed to be curvilinear. An identical trend was found when six-month-old heifers were used and the dietary energy level was raised from 9.2 to 12.3 Mcal of crude ME per day at a constant crude protein intake of 1.0 lb. per day. In another trial (Broster et al., 1969) where yearling heifers were fed two levels of protein and energy, the basal ration supplied 0.82 lb. of starch equivalent per 100 lb. liveweight daily and 1.41 lb. of crude protein daily. This ration supported a daily liveweight gain of 0.47 lb. When additional energy was added to bring the level up to 1.20 lb. of starch equivalent per 100 lb. liveweight daily, with the same crude protein level, the daily gain was

increased significantly to 1.29 lb. per day. However when the crude protein level was boosted to 1.62 lb. per day with the basal energy level, the average daily gain was only 0.54 lb., which was not a significant increase, thus demonstrating the effect of limiting energy. Broster et al. (1963), Preston (1963) and Stobo et al. (1967a, 1967b) all expressed the view that the major factor determining rate of liveweight gain in calves and cattle may be the intake of dietary energy. These workers found that the response obtained by increasing protein intake at any one level of energy intake is only marginal.

Elliott et al. (1964) showed that the response (body weight gain or loss) to protein increments in the ration began to decline at a lower intake of protein with low than with high energy rations. Liveweight gain was significantly affected by the level of intake of digestible crude protein and total digestible nutrients, and also by a highly significant interaction between these dietary components. As the level of protein increased, the estimated amount of TDN required by African steers for maintenance declined. Noland and Scott (1960) found that the weight gains in young pigs from 40 to 75 lb. was affected not only by the protein level, but also by a significant protein-energy interaction. Andrews and Ørskov (1970a) found a significant interaction occurred with lambs whereby growth increased with higher protein concentrations as feeding level increased. They also found linear increases in the rate of protein deposition and decreases in fat deposition in the carcass with increases in the concentration of crude protein (Andrews and Ørskov, 1970b). This effect was particularly marked at the high level of feeding. Gardner (1968a) reported a significant interaction between protein and energy levels on feed efficiency in young Holstein heifers. In this instance, protein and energy levels were varied using meat meal and stabilized fat.

Using two-year-old barren heifers, Broster et al. (1969) found that additional dietary protein increased the digestibility of protein in the diet, but that the additional

dietary energy decreased the digestibility of protein. These results are in line with those reported by several other workers. Head (1953), Williams et al. (1953), Tagari et al. (1964), and Head and Murdoch (1965) all reported that additional protein increased the digestibility of protein and fibre, but that additional energy had the reverse effect in both sheep and steers.

Protein:Energy Ratios

In going a step beyond interrelations or interactions between protein and energy, let us now consider these nutrients in terms of a ratio. As mentioned earlier, the basis of Henry's (1904) "nutritive ratio" (cited by Crampton, 1964) was the proportion of protein to carbohydrate equivalent in the diet. In the hog diets formulated by Noland and Scott (1960), they found that low calorie:protein ratios resulted in best gains when animals were younger, but that higher calorie:protein ratios produced best gain when the animals were older. This substantiates Blaxter and Wood's (1951) concept that the protein:energy ratio does not remain constant as the animal matures. Wagle et al. (1962) found in rats that as the dietary ratio of energy to protein decreased, the fat content of the body decreased. They also found that the xanthine oxidase in the livers of animals given the diets with the lower calorie:protein ratios, caused by the addition of cellulose, was reduced. This was a reflection of the protein quality of the diet. Prés (1964) reported that gains in cattle were highest with wide energy:protein ratios. Shenk and Elliott (1968) studied the effect of energy and protein on growth in the weanling meadow vole, and found a specific protein:energy ratio for this animal. Any deviation from this balanced relationship resulted in growth depression.

Many workers have tried to be very specific with regards to the actual ratios used. Epley et al. (1970b) used ratios of 10.1, 22.1, and 27.6 grams of digestible protein (DP) per Mcal of digestible energy (DE) in rations for Hereford

steer calves. They found that as the DP:DE ratio increased, days on feed up to 453.9 kg. decreased, average daily gain and feed consumption increased, and kilograms of retail cuts, fat trim, and bone developed per day increased. Kilograms of muscle protein gained per day also increased. Protein efficiency decreased as the DP:DE ratio increased.

Crampton (1964) gave the protein:energy ratio for adult cows at maintenance as 19.3 g. DP per 1000 kcal of DE. This is fairly close to the general ratio he proposed for adult ruminants and swine of approximately 25 g. DCP per 1000 kcal of DE (Crampton, 1965).

In Gardner's work (1968a) with young Holstein heifers, he established that a protein:energy ratio of around 31.5 g. DP per Mcal of DE was the most satisfactory for calves between 68 and 110 kg. when fed free-choice. This higher protein:energy ratio for younger animals is in agreement with Guilbert and Loosli (1951).

Gardner (1968b) reported that ratios of estimated net energy (kcal) to crude protein (%) for dairy calves ranged from 64.3 to 47.4 to one, with no distinguishable effect on rate of gain or feed efficiency. These results are not compatible with the conclusions of Brown and Lassiter (1962) that the ratio should be 46:1 or less for optimal performance on calf starters.

Preston (1966) reported the protein to energy ratios required in the rations of growing-finishing cattle and lambs for various rates of growth. He felt that this ratio was more a function of the rate of gain than the portion of mature weight that had been attained. His proposed ratios ranged from 20.8 to 27.8 g. DP per Mcal of DE for cattle at maintenance to a gain of two kg. per day, respectively. Preston's (1966) ratios are in fairly close agreement with Crampton (1964) who estimated the intraspecies maintenance ratio at 19 to 20.

Preston (1969) used protein:energy ratios of 28, 22 and 10 g. of DP per Mcal of DE for animals in the weight range of 500 to 1000 lb. The difference

between the medium and high protein to energy ratio did not begin to occur until midway through the feeding period. The lowest gains for calves fed the low ratio occurred during the first 50 days, whereas their gain during the last 100 days paralleled that observed on the medium protein:energy ratio.

All of this research points to the importance of relating protein requirements with energy. Balch (1967) found that as long as protein was limiting, the animal response to more protein was rectilinear. If protein is added to a diet in which energy is limiting, the animal may respond, but not as much as when energy is not limiting. The diminishing response per unit of protein can be attributed to the use of protein as an energy source. At low levels of energy, additional nitrogen may not be beneficial at all. Maximum responses to added nitrogen are to be expected only in animals which are on the rectilinear part of the response curve.

Broster et al. (1969) summarized this concept by saying that protein requirements for a given rate of production depend on the intended energy intake. Conversely, given levels of protein will promote various rates of production, not just one level. Elliott et al. (1964) similarly stated that a single value for the protein requirement for maintenance of cattle may not be either useful or valid, as for a given liveweight change the level of protein required depended on the level of energy in the ration. Hence, they concluded that protein requirements could be defined only when the amounts of digestible energy contained in the diet are known. This is also in agreement with the conclusion of Broster et al. (1963).

Considerations with Respect to Ruminants

Much of the work concerning the associative effects of protein and energy has been done on the monogastric (Allison et al., 1946; Munro, 1951; Munro and Naismith, 1953; Hill and Dansky, 1954; Calloway and Spector, 1955; Donaldson et al., 1956; Clawson et al., 1962; Yoshida et al., 1970). There are, however,

several factors which should be taken into consideration when concepts from monogastric work are applied to ruminants.

Inasmuch as the ruminant's food supply is intercepted by the rumen microorganisms, the quantity and quality of nutrients ultimately offered to the host animal are quite different from those which were ingested. Thus, the optimum ratio of protein and energy which the ruminant receives is dependent on supplying an optimum protein:energy ratio to the rumen microorganisms. If there is not sufficient energy supplied to the microbial population, it will not exhibit normal growth, and hence will have a decreased need for protein for cellular growth. Therefore, nitrogen freed in the rumen from proteolysis may not be incorporated into microbial tissue and may be lost as urea excreted in the urine. On the other hand, if there is a shortage of nitrogen available for microbial growth, this would retard growth, which would in turn tend to inhibit carbohydrate fermentation with its release of energy-yielding nutrients. There is some discrepancy with regards to the effect of the addition of dietary energy on the rumen microbial population. Tagari et al. (1964) found that nitrogen retention decreased when starch was substituted for roughage carbohydrates in the ration. It was felt that this was due to an increased rate of ammonia liberation. A significant correlation ($r=-0.909$) was found between blood urea concentration and nitrogen retention. On the other hand, Broster et al. (1969) found that an increase of starch in the ration raised nitrogen retention, but that the addition of oat hulls tended to decrease it. At any rate, it is quite clear that the balance between ammonia release and ammonia absorption or incorporation is quite critical in the rumen.

Another complication that occurs as a result of the microbe-ruminant symbiosis is the difference in metabolic efficiencies. The anaerobic populace of the rumen is somewhat inefficient in metabolizing foodstuffs. According to Hungate (1966) anaerobic microorganisms usually can only synthesize about ten percent of

the carbohydrate substrate into protoplasm. The ruminant, being an aerobe, is much more efficient in this respect, plus the fact that the ruminant can utilize the volatile fatty acids (VFA) from rumen fermentation of carbohydrate for energy. Thus, the ruminant, because of its greater energy supply has the potential for greater synthesis of protein, but the interception of its food supply by the rumen microorganisms makes it dependent on the protein synthesized in the anaerobic microbial metabolism. Thus, the ruminant may find itself in a chronic protein deficiency relative to energy.

A sidelight to this problem is the possibility of "protecting" protein from microbial attack in the rumen. This would allow the ruminant to make use of the feed protein directly, without the intermediate step of assimilation into microbial protein. Such a method of protection would of course be only used for proteins of very high nutritional quality. The possibilities for rumen bypass or protection are many, (Ørskov and Benzie, 1969; Scott et al., 1970), and could, should such methods become commercially available, have quite an important impact on our present ideas of optimum protein and energy levels or ratios.

Still another complication is the fact that the rumen population is a dynamic one. It is constantly subject to change -- both in terms of species present, and in terms of the phase of growth. Hence, the nutritional requirements of the population as a whole may change from time to time.

Ruminants also differ from monogastrics inasmuch as their principal metabolites from the diet differ (Munro, 1951). The fact that ruminants use VFA as a major source of energy (65-75% (Hungate, 1966)) rather than glucose, and the fact that blood ammonia and urea levels are elevated in ruminants may have a bearing on the optimum protein:energy ratio at any given protein or energy level.

In ruminants, due to the fact that the diet is often composed of very fibrous material, the rumen size and the rate of passage of material through the rumen often are limitations to feed or energy intake. Thus, eating food to main-

tain a relatively constant intake of energy may not be as easily accomplished as in the monogastric. There are currently several theories on appetite control which may be applied to the ruminant, and it would seem that the actual mechanism may be a combination of several of the proposed theories (Brobeck, 1957; Mayer, 1957; Duckworth and Shirlaw, 1958; Kennedy, 1961). At any rate, it is quite clear that this factor is certainly a complicating factor in the consideration of protein and energy levels for ruminants.

EXPERIMENTS AT THE UNIVERSITY OF ALBERTA

Introduction

In order to study the effects of different protein to energy ratios in diets for fattening steers, an experiment was designed using Holstein steers fed rations based on barley. Three ratios of protein to energy were used. Studies on growth rate and feed consumption were carried out over a period representing approximately 100 kg. of gain on each steer. About midway through the feeding period, metabolism trials were carried out to determine digestibility and retention of protein and energy. Carcass data on all steers was collected at slaughter, and physical and chemical analyses were done on the tenth rib section of each steer.

Experimental

Design

The experimental design chosen was factorial, with three levels of protein and three levels of energy for a total of nine treatment combinations. Three steers were used for replication in each treatment combination.

Animals and Management

Twenty-seven Holstein steers, averaging 319 kg. liveweight were purchased near Edmonton and trucked to the Edmonton Research Station, University of Alberta. The weights ranged from 281 to 381 kg. They were divided into three liveweight groups of light, medium, and heavy steers. Each of the nine steers in each weight group was then randomly assigned to one of the nine possible treatment combinations.

The steers were housed in the Dairy Cattle Research Unit, and were tied in individual stalls over slatted flooring. Fresh water was available free-choice.

To allow the steers to adjust to their new surroundings before the trial began, they were offered a daily ration of greenfeed and rolled oats, free choice, for one week. Aureo S-700 was fed to the steers for the first 21 days at a level of 700 mg. per day to counteract stress and reduce the incidence of shipping fever. All steers received an intramuscular injection of 500,000 International Units (I.U.) of vitamin A, 75,000 I.U. of vitamin D, and 50,000 I.U. of vitamin E upon arrival at the farm.

After the adjustment period of one week, the steers were offered the experimental rations and were brought up to full-feed. The procedure used was to feed 1.5 percent of the steers' body weight in kilograms in two equal feedings per day. Then, each steer was increased by 0.2 kg. of feed per feeding until full-feed was reached. Any steer that failed to consume its portion of feed was cut back until it did so, and the increasing procedure was then repeated. Generally, the rations were fed in equal portions at 8 A.M. and 5 P.M. All feed and unconsumed feed was weighed and recorded daily.

Salt and minerals were not offered free-choice to the steers at any time during the trial, as it was felt that adequate amounts of these were supplied in the experimental rations. Also, it was felt that excessive salt and/or mineral intake might grossly affect water consumption and urine output, which might affect the metabolism studies.

All steers were weighed every four weeks throughout the trial, and more frequently as they neared 100 kg. gain. They were weighed in the morning before feeding, after water had been withheld for three hours.

Experimental Rations

The three experimental rations were high-concentrate rations composed primarily of barley. On the basis of ingredient analysis, ration 1 was formulated to be low protein (8.9 percent crude protein), ration 2 to be medium protein (11.8

percent crude protein), and ration 3 to be high protein (14.7 percent crude protein). Analysis of samples of the rations showed they contained 8.7, 11.9, and 14.2 percent crude protein, respectively (Table 1). The increments of crude protein were attained by substitution of soybean meal for barley in the medium and high protein rations. All rations were formulated to be approximately isocaloric.

The barley was coarsely rolled, and the limestone, salt, and vitamin ADE were added as a premix. Fresh rations were prepared weekly and were sacked from the feed mixer to reduce physical separation of the ingredients.

Energy Restriction

Energy intakes of the steers were varied by means of restricting total consumption, as it was felt that this would introduce less error than ration dilution with a high-fibre material.

Each ration was fed at three levels: full-feed, 90% of full-feed, and 80% of full-feed. Once the full-feed level for each ration was established by the previously mentioned procedure, three steers were allowed to continue consumption of the ration at full-feed (high energy), three steers were restricted to 90% (medium energy) of the amount eaten by the full-fed group the previous week, and three steers were restricted to 80% (low energy) of the amount eaten by the full-fed group the previous week.

Metabolism Studies

Metabolism studies were conducted on one steer drawn randomly from each treatment combination after the different levels of energy had been in effect for eight weeks. The nine steers were moved to another area of the barn where the gutter grates could be removed to facilitate urine collection. They were again individually stalled and were allowed to adjust to these surroundings for ten days before feces and urine collections began. Adjustments of feed consumption were

TABLE 1. Ration formulations and analysis

Ration Ingredients (Kg. or %)	1. LOW PROTEIN	2. MEDIUM PROTEIN	3. HIGH PROTEIN
Barley	87.50	79.25	71.00
Soybean meal		8.25	16.50
Beet pulp	10.00	10.00	10.00
Limestone	2.00	2.00	2.00
Cobaltized-iodized salt	0.50	0.50	0.50
Vitamin ADE ¹	0.088	0.088	0.088
Total	100.000	100.000	100.000

Analysis - Actual

Dry matter %	87.8	87.9	88.0
Crude protein (air dry basis)%	8.7	11.9	14.2
Gross energy (air dry basis) Mcal/kg.	3.76	3.73	3.78

¹ Vitamin ADE: supplies 8800 I.U. vitamin A, 880 I.U. vitamin D, and 88 I.U. vitamin E per kg. of ration.

not made to any of the 27 steers during the five-day period while collections were being made.

The urine collection apparatus was similar to that used by Malmberg (1972). Urine was collected in ten-litre nalgene bottles, which were suspended from the gutter grates so that they were beneath floor level. Hydrochloric acid (50% v/v) was used as a preservative in amounts sufficient to lower the pH to a value of two. Urine volumes were measured and recorded every 24 hours, and five percent was retained as a sample. Urine samples from each steer were composited, frozen in nalgene jars at -10°C ., and stored for later analyses.

The fecal collection apparatus used was based on collection bags developed by Malmberg (1972). The polyethylene bags used in this study measured 41 cm. by 152 cm., and were long enough to permit them to be strapped over the back of the animal. This resulted in more stability of the collection bag and better weight distribution. Total feces was weighed and recorded twice daily at 8 A.M. and 8 P.M. Five percent was retained and frozen from each collection. At the end of the trial, the composite sample from each steer was dried at 55°C . for 72 hours in a forced-draught Despatch oven. The sample was then allowed to equilibrate with the atmosphere for 48 hours before weighing and subsequent grinding in a Waring Blender. Samples were then stored for later analyses.

Samples of the experimental rations were collected daily during the metabolism trials, composited, ground in a Wiley laboratory mill, and retained for later analyses.

Carcass Measurements

Farm weights of all the steers were recorded before they were trucked to the packing plant (a distance of three miles). The weights were taken the morning the steers were to be slaughtered, after being without water for three hours.

Viscera abnormalities were noted and recorded as the steers were slaughtered, and the weight of kidney fat from the left side of the carcass was recorded.

Following government grading of the animals, 24 hours after slaughter, the 9-10-11 rib section was removed from the right side of the carcass. The tenth rib section was then separated from the standing rib by a standardization procedure described by Malmberg (1972). The tenth rib section was then physically separated into separable fat, lean, and bone. The fat and lean samples from each steer were frozen at -10 C. and stored for later analyses.

Analytical Methods

Dry matter and crude protein were determined on the feed and fecal samples, and crude protein was determined on the urine samples by AOAC (1965) methods. The dry matter of the urine was determined by freeze-drying a five-ml. sample for 96 hours on a Virtis freeze-dryer.

Gross energy of feed and fecal samples, and of freeze-dried urine samples was determined by combustion in a Parr oxygen bomb calorimeter. Feed and fecal samples were combusted at 25 atmospheres of oxygen, but urine samples had to be combusted at 30 atmospheres of oxygen to facilitate complete combustion.

Both fat and lean samples were first diced, then dried for 96 hours at 30 microns of mercury pressure and -70 C. on a Thermovac freeze-dryer. Dry matter, ether extract, and crude protein determinations on the lean samples were then carried out by AOAC (1965) methods. A partial ether-extraction was done on the freeze-dried fat samples by blending and repeated washings with hexane, prior to a crude protein determination by the macro-Kjeldahl method.

Statistical Analyses

An IBM MTS computer in the Department of Computing Science, University

of Alberta was used to statistically analyze the data. A two-way analysis of variance APL program, AOV5 (Smillie, 1969b), was used to determine significance. Duncan's New Multiple Range Test (Steel and Torrie, 1960) was used to compare differences between means. The data from one steer in the low protein-low energy treatment had to be discarded as the steer was sick throughout the trial. The mean value of the other two steers in this group was substituted for this missing data, and hence one degree of freedom was lost from the error term throughout the analyses. The mean squares are shown in the appendix.

The estimation of regression equations to describe a response surface for the data was done by APL programs developed by Smillie (1969a). Simple plots were also estimated by these programs. Only linear, interaction, and squared terms were considered for inclusion in the regression equation. The derivation of the equation to describe isoquants from quadratic equations is given in the appendix.

RESULTS AND DISCUSSION

Protein and Energy Intake

Steers fed the low, medium, and high protein levels consumed an average of 602, 855, and 991 g. of crude protein per day, respectively, throughout the trial (Table 2). These means were significantly different from each other ($P < 0.05$). Thus, the dietary crude protein intake for each protein level was different, as was planned. The level of energy fed significantly affected ($P < 0.05$) protein intake. The steers in the high energy group consumed more crude protein than those in the low energy group, and the steers in the low energy group consumed the least crude protein. Differences in dietary crude protein intake due to the energy level fed was a consequence of the fact that energy restriction was accomplished by feed restriction, and thus dietary crude protein was restricted also.

Steers fed the high, medium, and low levels of energy consumed an average of 29.4, 26.0, and 23.5 Mcal of gross energy per day, respectively, throughout the trial (Table 2). The high energy group consumed significantly more energy ($P < 0.01$) than the other two energy groups. The low and medium energy groups consumed 79.8 and 88.5 percent, respectively, of the energy consumed by the high energy group, and hence the difference between the low and medium energy levels was not as great as had been planned. The level of crude protein fed had no effect on the energy intake ($P < 0.05$). No differences had been expected here as all rations were approximately isocaloric.

Average Daily Gain

The average daily gains for steers receiving the low, medium, and high protein levels were 0.70, 0.78, and 0.78 kg., respectively, and were not significantly different ($P < 0.05$) from one another (Table 3). The average daily

TABLE 2. Intake of crude protein and gross energy

Energy Level		Crude Protein Level			
		Low	Medium	High	
Protein Intake (g./day)					
High		692.5	935.3	1100.8	average 909.5 ^A
Medium		566.5	863.6	1008.0	812.7 ^{AB}
Low		547.4	765.4	865.4	726.1 ^B
	average	602.1 ^A	854.8 ^B	991.4 ^C	
Energy Intake (Mcal/day)					
High		29.8	29.2	29.2	average 29.4 ^b
Medium		24.4	27.1	26.8	26.0 ^a
Low		23.6	23.9	23.0	23.5 ^a
	average	25.9 ^A	26.7 ^A	26.3 ^A	

a, b means in the same group which are followed by a common superscript are not significantly different ($P < 0.01$).
A, B, C means in the same group which are followed by a common superscript are not significantly different ($P < 0.05$).

TABLE 3. Average daily weight gain

Energy level	Crude Protein level			average
	8.7%	11.9%	14.2%	
Average daily gain (kg.)				
High	0.86	0.94	0.95	0.91 ^a
Medium	0.72	0.72	0.76	0.74 ^{ab}
Low	0.53	0.67	0.63	0.61 ^b
average	0.70 ^A	0.78 ^A	0.78 ^A	

a, b, means in the same group which are followed by a common superscript are not significantly different. ($P < 0.01$)

A means in the same group which are followed by a common superscript are not significantly different. ($P < 0.05$)

gains for steers receiving the high, medium, and low energy levels were 0.91, 0.74, and 0.61 kg., respectively. Daily gains by steers fed the high level of energy were significantly higher ($P < 0.05$) than gains made by those in the other two groups, and gains made by steers fed the low level of energy were significantly lower ($P < 0.01$) than gains made by those in the high energy group.

In general, the daily gains by these steers were low, as the overall average was only 0.75 kg. Preston et al. (1963b) reported Holstein steers fed a very similar diet for a similar feeding period gained an average of 1.18 kg. per day. Holstein steers fed a ration based on barley to a slaughter weight of 350 kg. were found to gain approximately 1.2 kg. per day, as reported by Kay et al. (1968). Kliewer et al. (1970) reported daily gains of 1.07 and 1.20 kg. per day by Holstein steers on test from 114 kg. to 500 kg. and fed rations containing 11 and 15 percent crude protein, respectively. Even in studies where yearling Friesian steers were fed various levels of chopped or ground straw (Swan and Lamming, 1970; Kay et al., 1970a, 1970c), the average daily gains were in excess of 1 kg. per day.

The effects of dietary crude protein and gross energy on average daily gain are shown in Figure 3. The response in daily gain for protein levels is shown with gross energy intake as the ordinate, and the response for energy levels is shown with crude protein intake as the ordinate. Average daily gains show a diminishing response with increased energy at the low protein level, but increasing returns to scale response with increased energy at the medium and high protein levels (Figure 3). The curves showing daily gain response at various energy levels with increased crude protein indicate a diminishing response at the high energy level, a slight increase at the medium energy level, and a parabolic-type of response at the low energy level.

This indicates that at the low protein level, increases in dietary energy show less and less benefit, as protein becomes the limiting factor for growth. This response is analagous to the protein limitation of response to increased energy as in the area to the right of point B, Figure 1 (Calloway and Spector, 1954). The increasing slopes of the curves for medium and high protein indicate that energy was extremely beneficial in these instances as represented in the area to the left of point A in Figure 1. It would be expected that the response to medium and high protein would exhibit a diminishing return to scale function if a higher level of energy were to be fed.

The curve describing the gain response of the steers receiving the high energy level indicates that energy was the limiting factor to increased gains when crude protein was increased. At the medium energy level, there were essentially no differences, as an increase in protein from the low to medium level did not affect daily gain at all, and an increase from the medium to high protein level resulted in only slightly higher gain. This response is probably due to animal variation. The curve describing the response of the steers to the low energy level indicates that a maximum response to protein was reached at the medium protein

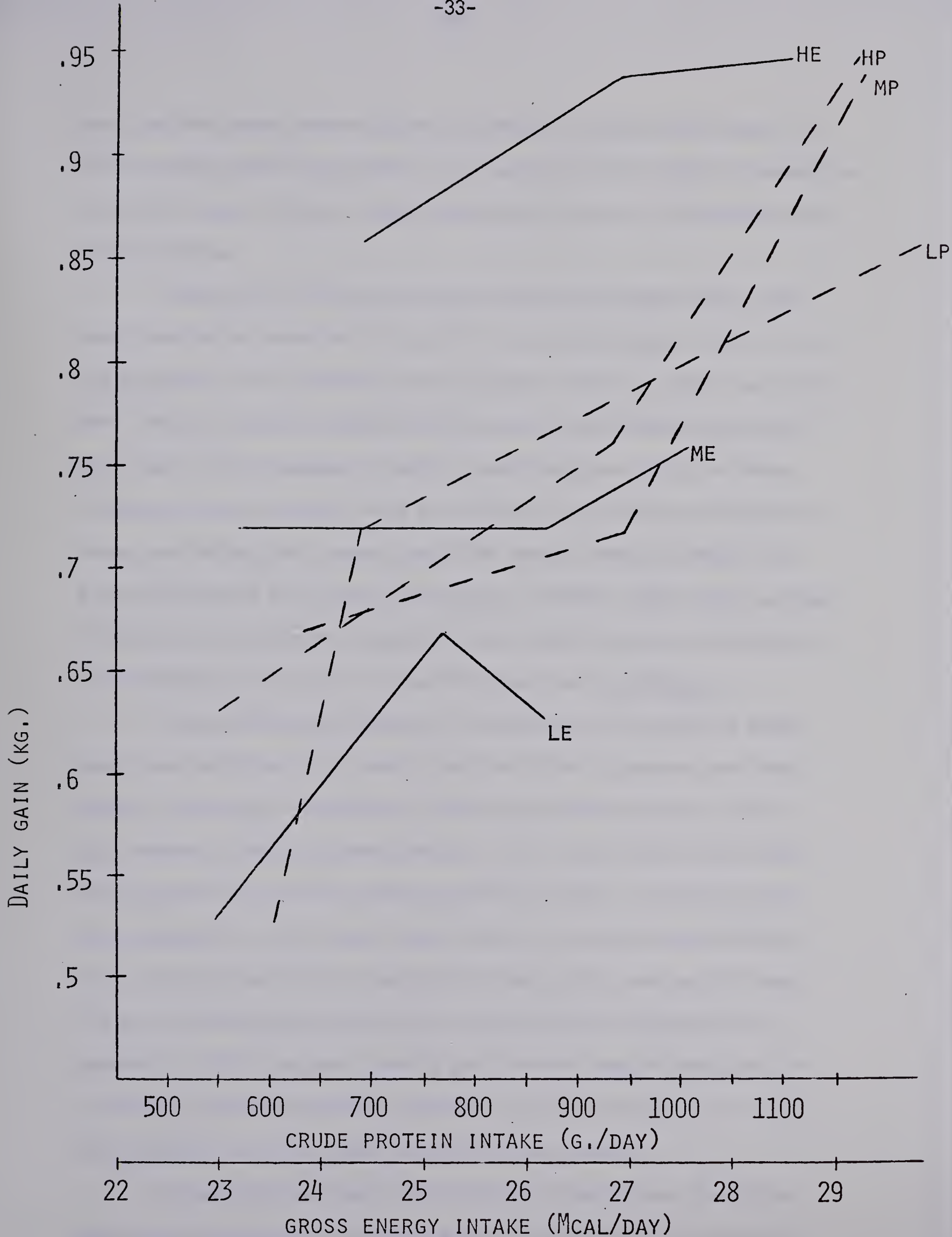


FIGURE 3. THE EFFECT OF DIETARY CRUDE PROTEIN AND GROSS ENERGY ON AVERAGE DAILY GAIN (H, M, L = HIGH, MEDIUM AND LOW, RESPECTIVELY; P, E = PROTEIN, ENERGY, RESPECTIVELY)

level, and that growth rate was depressed slightly at the high protein level. At this low energy level, there possibly was not enough energy available to metabolize any protein excess. However, these differences are very small and probably due to animal variation.

Stobo et al. (1967a) have also documented a case where dietary crude protein was limiting when fed at a low level, even though energy intake was on an ad libitum basis. This is similar to the trend shown for the low protein level in this trial. The gain response to medium and high protein in this study indicates that more energy might be necessary to obtain even higher gains. Balch and Bines (1968) tested several nitrogen levels with 388-kg. Friesian heifers and found that energy was limiting at all, except possibly the lowest, levels of nitrogen input. A very similar result was reported by Stobo et al. (1967a). When calves were fed a 19.2 percent crude protein concentrate (high protein), energy was found to be the limiting factor even when the concentrate was offered ad libitum.

The curvilinear-type response to increasing levels of protein at a high energy level exhibited by the steers in this trial is also in agreement with other research. Broster et al. (1969) found with two-year-old non-pregnant heifers little response to additional protein above 1.71 lb. crude protein per day when the energy level was 0.95 lb. starch equivalent per 100 lb. liveweight per day. Also, using yearling heifers these workers found at an energy level of 0.82 lb. starch equivalent per 100 lb. liveweight daily and a daily crude protein intake of 1.4 lb., the daily gain was 0.47 lb. When the dietary crude protein was increased to 1.62 lb. per day, the daily gain increased nonsignificantly to 0.54 lb. Raleigh and Wallace (1962), and Malmberg (1972) both found that at high energy intakes, low protein levels limit growth quite severely.

The possible trend found in this trial for maximal gains at the medium rather than the high protein level when energy was restricted to the low level

has also been reported elsewhere. Balch (1967) stated with reference to ruminants that at low energy levels, additional nitrogen may not be beneficial at all in improving nitrogen balance or body weight gain. Elliott et al. (1964) found that on a high protein - low energy combination diet, steer gains were depressed more than on a medium protein - low energy diet. The same is true for this trial (Figure 3).

The low, medium, and high crude protein rations fed in this study (8.7, 11.9, and 14.2 percent crude protein, respectively) resulted in three crude protein to gross energy ratios of 23.2, 32.0, and 37.6 g. of crude protein per Mcal of gross energy, respectively. Thus, in terms of protein to energy ratios, the wider ratios of 32.0 and 37.6 resulted in slightly better average daily gains than the narrow ratio of 23.2. This trend is substantiated by Epley et al. (1970b) who found that average daily gains of fattening Hereford steers were increased with increases in the protein to energy ratio. Zimmerman et al. (1961) found with Hereford-Angus fattening steers that a narrow ratio of energy to protein resulted in best gains. This is in agreement with Epley et al. (1970b) and the data from this trial. However, Epley et al. (1970b) used protein to energy ratios that were lower than used in this study. From the results obtained here, it would indicate that a protein to energy ratio of 32.0 g. of crude protein per Mcal of gross energy is sufficient to support the rate of growth obtained in this trial. This ratio seems to be slightly higher than required ratios reported by Preston (1966), Gardner (1968a), Preston (1969), and Epley et al. (1970b). However, when converted to a ratio of g. of digestible protein per Mcal of digestible energy by assuming a crude protein digestibility coefficient of 57.9 percent and a gross energy digestibility coefficient of 62.4 percent (Table 7), this optimum ratio becomes approximately 29.6. This value is fairly close to the National Academy of Sciences-National Research Council (1963) recommendation for this class of livestock of 26.2 g. of digestible

protein per Mcal of digestible energy.

Matsushima et al. (1957) fed three levels of protein and energy to yearling Hereford steers to evaluate various protein-energy ratios for fattening steers. Their results showed that the steers on the high protein-medium energy diet had the highest gain. Jones and Hogue (1960) did a similar trial with lambs, using two levels of protein and energy and found the highest gains occurred on the high protein-high energy diet. The results of the present study showed highest gains were attained at the high protein-high energy and medium protein-high energy levels. The gains were essentially the same at these levels.

In an attempt to describe the effect of dietary crude protein and gross energy on average daily gain in terms of a response surface, the independent variables crude protein intake (g./day) and gross energy (Mcal/day) were fitted in a multiple regression equation to predict the dependent variable, gain (kg./day). The multiple regression equation obtained was:

$$Y = 1.099 + 2.935E^{-4}X_1 - 7.137E^{-2}X_2 - 8.939E^{-7}X_1^2 + 1.223E^{-3}X_2^2 + 4.846E^{-5}X_1X_2 \quad (1)$$

where Y = gain (kg./day)

X_1 = crude protein intake (g./day)

X_2 = gross energy intake (Mcal/day)

The coefficient of determination, $100R^2$, for this equation was 68.1%, and the F-value was 8.98 ($P < 0.01$). However, the opposite signs for the X_1 squared term and the X_2 squared term indicate that the predicted response surface takes the shape of a saddle-shaped curve. This is because the gain response to crude protein shows diminishing returns to scale, whereas the gain response to gross energy shows increased returns to scale. However, none of the t-values for these regression coefficients approached statistical significance. Therefore, it was

decided to attempt to describe the dependent variable in terms of the independent variables on the basis of inputs per metabolic weight (M.W.). The multiple regression equation so obtained was:

$$Y = 3.201 + 5.314E^{-2}X_1 - 2.005E^{-2}X_2 - 1.020E^{-2}X_1^2 + 2.791E^{-5}X_2^2 + 5.001E^{-4}X_1X_2 \quad (2)$$

where Y = gain (kg./day)

X_1 = crude protein intake per unit metabolic weight (g./W_{kg.} 3/4/day)

X_2 = gross energy intake per unit metabolic weight (kcal/W_{kg.} 3/4/day)

The coefficient of determination for this equation was 67.4% and the F-value was 8.68 ($P < 0.01$). For this equation, the t-value for the regression coefficient of X_2 was statistically significant ($P < 0.05$), and the t-value for the X_2 squared term was statistically significant at a lower probability level ($P < 0.20$). Again, this prediction equation describes a saddle-shaped curve, as the X_1 squared and X_2 squared coefficients are of opposite sign. It was felt that equation (2) was the more valid equation to use because of its more significant t-values, even though the R^2 value and the F-value were slightly lower than for equation (1). Using this equation, predicted values were calculated at average daily gains of 0.7, 1.0, and 1.2 kg. per day. The isoquants for these gains are shown in Figure 4. Note that values to the right of the minimum displayed by the curve are not economical, as protein would be wasted at these levels.

A simple economic study was attempted to determine the relative amounts of crude protein and gross energy that would be used for a daily gain of 0.7 kg., if, for example, crude protein cost 0.035 ¢ per g. and gross energy cost 0.72 ¢ per Mcal. These nutrient costs would then have a price ratio of 48.6 kcal of gross energy per g. of crude protein. The solution was sought at the point where the first derivative of the isoquant equation was equal to -48.6. However, due to the nature of this curve, it only approached a maximum slope of approximately -30.

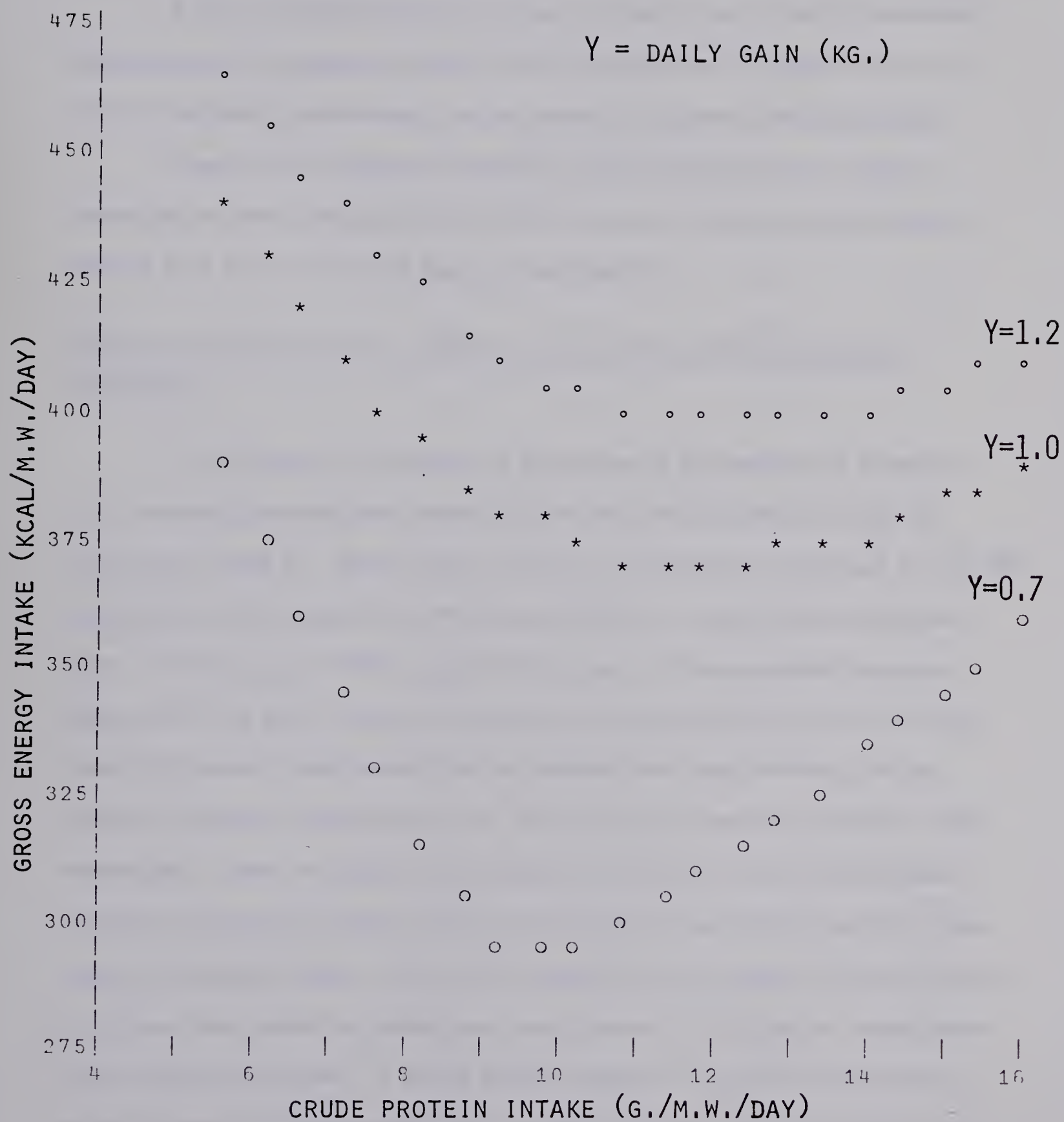


FIGURE 4. GAIN ISOQUANTS FOR CRUDE PROTEIN AND GROSS ENERGY INPUTS PER METABOLIC WEIGHT

The economic implication is that energy, in this example, is the preferred nutrient input as far as costs are concerned, and as much energy would be used as possible.

It may be noted here that the curves in Figure 4 are limited approximately by the range of the experimental data, and do not necessarily represent either the widest or narrowest protein-energy ratios capable of supporting the gains shown.

There were no differences between treatment groups either in initial liveweights or final liveweights ($P < 0.05$), but days on feed were significantly reduced ($P < 0.01$) in the high energy group (Table 4).

Efficiency of Utilization of Dry Matter, Crude Protein, and Gross Energy for Weight Gain

The efficiency of utilization of dry matter for liveweight gain increased with increasing levels of crude protein and decreased with decreasing levels of gross energy (Table 5). These trends, although not statistically significant ($P < 0.05$), are the same as those reported by Malmberg (1972) for younger Holstein bulls and steers. Kliewer et al. (1970), using Holstein steers in the same weight range as those used in this study, also found the feed conversion of steers receiving the high protein (15 percent crude protein) diet to be better than those receiving the low protein (11 percent crude protein) diet. The feed conversions were 6.88 and 7.88, respectively. Jones and Hogue (1960) found the same trend with fattening lambs, as lambs receiving high protein diets had more efficient feed conversions than those receiving low protein diets. Lister (1970) reported no improvement in feed efficiency of Holstein steers when the protein level was in excess of 12.5 percent crude protein in all-concentrate rations. A similar trend is apparent in the data from this study, as the increase in dry matter efficiency was very small when the crude protein level was increased from 11.9 percent to 14.2 percent. Malmberg (1972) also reported very little or no improvement in feed efficiency over the 12.99 percent crude protein

TABLE 4. Average initial and final liveweights and days on feed

Energy Level		Crude Protein Level			
		8.7%	11.9%	14.2%	
Initial Weights (kg)					
					average
High		313.2	323.7	316.5	317.8 ^A
Medium		327.5	324.3	318.7	323.5 ^A
Low		306.8	312.5	330.5	316.6 ^A
	average	315.8 ^A	320.2 ^A	321.9 ^A	
Final (Slaughter) Weights (kg)					
					average
High		402.5	424.5	423.3	417.7 ^A
Medium		426.5	414.8	420.7	420.7 ^A
Low		382.8	398.2	420.7	400.6 ^A
	average	404.8 ^A	412.5 ^A	421.6 ^A	
Days on Feed					
					average
High		110.7	108.0	117.7	112.1 ^a
Medium		138.3	126.7	133.7	132.9 ^b
Low		143.0	126.7	143.0	137.6 ^b
	average	130.7 ^A	120.4 ^A	131.4 ^A	

a, b

means in the same group which are followed by a common superscript are not significantly different ($P < 0.01$).

A

means in the same group which are followed by a common superscript are not significantly different ($P < 0.05$).

level. In general, the efficiency of utilization of dry matter for liveweight gain was poor for the steers on this trial. Preston et al. (1963b) reported a feed conversion of 4.76 (air-dry basis) for Holstein steers fed from 90 kg. to 405 kg. on a 13.2 percent crude protein diet composed of 85 percent barley.

The efficiency of utilization of dietary crude protein for liveweight gain (Table 5) was significantly affected by both protein intake ($P < 0.01$) and energy intake ($P < 0.10$). The low, medium, and high protein groups consumed 0.89, 1.12, and 1.30 kg. of crude protein per kilogram of liveweight gain, respectively. These means were all significantly different from one another ($P < 0.05$). The high, medium, and low energy groups consumed 1.02, 1.11, and 1.19 kg. of crude protein per kilogram of liveweight gain, respectively. The crude protein consumed per kilogram of liveweight gain was significantly lower ($P < 0.05$) for the high energy group than for the low energy group, and significantly higher ($P < 0.05$) for the low energy group than for the high energy group. Both Gardner (1968b) and Malmberg (1972) reported significant increases ($P < 0.05$) in the crude protein used per kilogram gain with increases in protein level with Holstein calves. Prés (1964) showed the same trend with Black Pied Lowland cattle. Gardner (1968a) showed that the crude protein consumption per kilogram gain was reduced when stabilized fat was added to the ration for Holstein calves. This is analagous to the results of this trial where the steers consuming the high energy levels had a lower crude protein consumption per kilogram gain, and also with results reported by Malmberg (1972) where the animals receiving the low energy levels had the highest consumption of crude protein per kilogram of gain.

The multiple regression equation describing the efficiency of utilization of crude protein for liveweight gain by steers in this trial is given by:

$$Y = 3.322E^{-1} + 2.498E^{-3}X_1 - 1.059E^{-2}X_2 + 1.210E^{-6}X_1^2 + 1.291E^{-3}X_2^2 - 1.256E^{-4}X_1X_2 \quad (3)$$

TABLE 5. Dry matter intake and efficiencies of feed utilization

Energy Level	Crude Protein Level			
	8.7%	11.9%	14.2%	
Average dry matter intake (kg./day)				
High	6.9	6.8	6.7	average 6.8 ^a
Medium	5.6	6.2	6.2	6.0 ^{ab}
Low	5.4	5.6	5.3	5.4 ^b
average	6.0 ^A	6.2 ^A	6.1 ^A	
Average dry matter intake per gain (kg./kg.)				
High	8.5	7.3	7.3	average 7.7 ^A
Medium	7.9	8.8	8.1	8.2 ^A
Low	10.2	8.3	8.5	9.0 ^A
average	8.9 ^A	8.1 ^A	8.0 ^A	
Average crude protein intake per gain (kg./kg.)				
High	.85	1.00	1.19	average 1.02 ^A
Medium	.80	1.21	1.32	1.11 ^{AB}
Low	1.03	1.14	1.39	1.19 ^B
average	.89 ^A	1.12 ^B	1.30 ^C	
Average gross energy intake per gain (Mcal/kg.)				
High	36.8	31.4	31.6	average 33.3 ^A
Medium	34.2	37.7	35.2	35.7 ^A
Low	44.5	35.8	36.9	39.1 ^A
average	38.5 ^A	35.0 ^A	34.6 ^A	

a, b means in the same group that are followed by a common superscript are not significantly different ($P < 0.01$).
A, B, C means in the same group that are followed by a common superscript are not significantly different ($P < 0.05$).

where Y = dietary crude protein required per kilogram of liveweight gain (kg. per kg.)

X_1 = dietary crude protein intake (g. per day)

X_2 = dietary gross energy intake (Mcal per day)

The coefficient of determination for this equation was 62.4% and the F -value was 6.96 ($P < 0.01$). The t -value for the coefficient of the X_1 term approached significance at the $P < 0.20$ level. As the coefficients for the X_1 squared and X_2 squared terms have the same sign, this curve does not follow a saddle-shape. Using this equation, predicted values were calculated for efficiency of crude protein utilizations of 0.9, 1.1, and 1.3 kg. of crude protein per kg. gain. The isoquants for these values are shown in Figure 5. From this graph, it can readily be seen that increasing the dietary gross energy at any given dietary crude protein level will result in less crude protein used per unit of gain. Also, increasing the dietary crude protein at any given dietary energy level will result in more crude protein used per unit of gain.

When crude protein is relatively cheap compared to gross energy, it is economical to decrease the gross energy input and increase the crude protein input (Figure 4). This, as seen in Figure 5, results in an increased usage of crude protein per unit of gain. Similarly, when crude protein is relatively expensive, the crude protein input would be decreased and the gross energy input increased, which would result in a decreased usage of crude protein per unit of gain. Hence, when crude protein is cheap, more is used per unit of gain, but at a lower cost per unit of protein; whereas when crude protein is expensive, less is used per unit of gain, but at a higher cost per unit of protein. Inasmuch as increased daily gains are attained in moving outward from the origin of the graph (increasing crude protein and increasing gross energy), it is conceivable that such a movement might be concurrent with an isoquant for efficiency of protein utilization. Thus, increased gains might be realized with no decrease in the efficiency of utilization of dietary

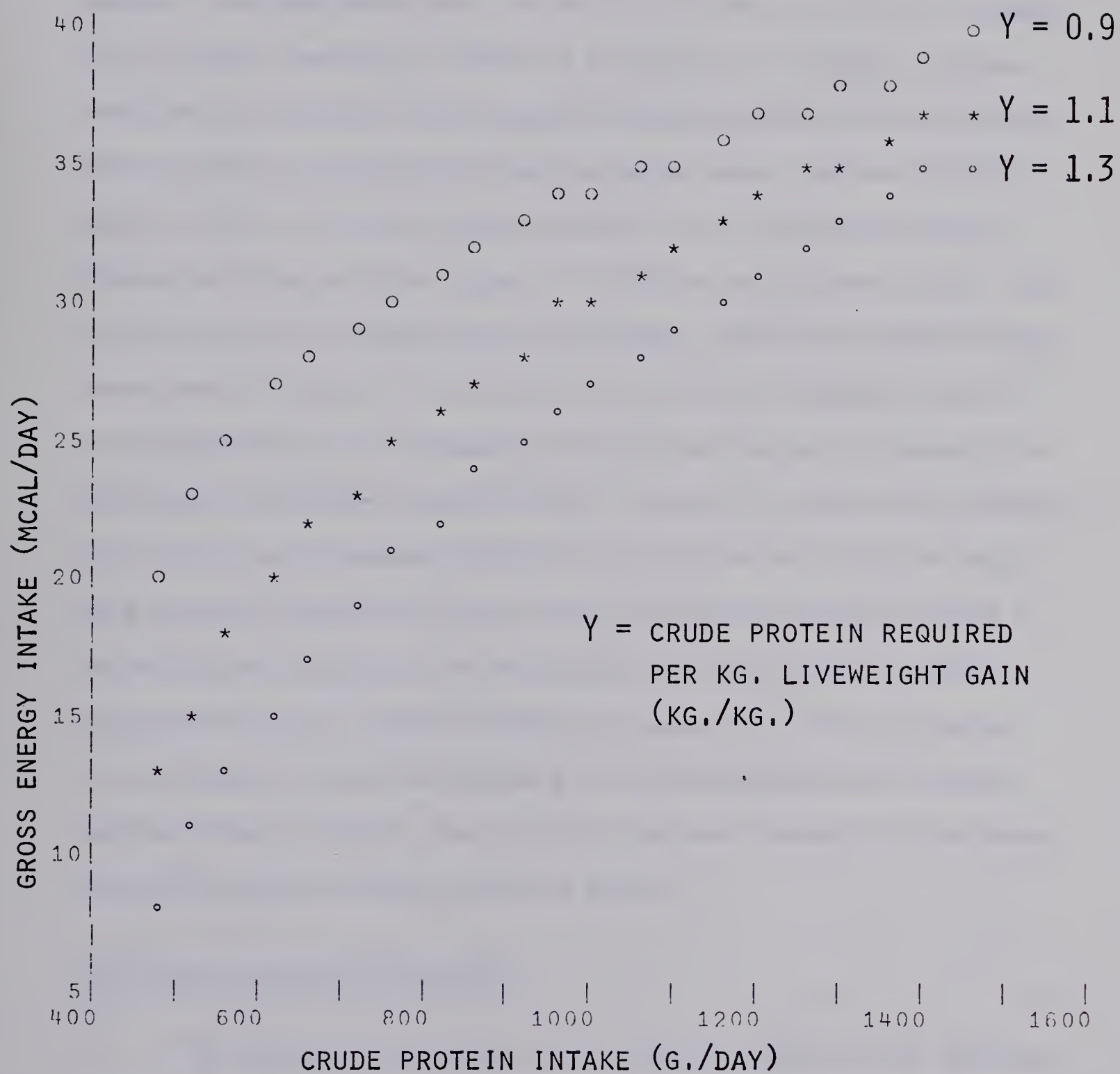


FIGURE 5. CRUDE PROTEIN PER GAIN ISOQUANTS FOR DAILY CRUDE PROTEIN AND GROSS ENERGY INPUTS

crude protein.

The efficiency of utilization of dietary gross energy for liveweight gains by the steers was not different ($P \leq 0.05$) for any of the treatment groups (Table 5). However, some trends are evident. As the level of dietary crude protein increased, the gross energy consumed per kilogram of liveweight gain decreased. The gross energy usage per kilogram of gain seemed considerably higher for steers receiving the low protein ration than for the other two protein levels. Malmberg (1972) found an identical trend using younger Holstein calves, with the gross energy consumed per kilogram of gain highest ($P < 0.01$) on the low protein ration. Prés, (1964) using Black Pied Lowland cattle and Gardner (1968a) using Holstein calves, both reported a reduction in the digestible energy used per kilogram of gain with increasing protein levels. Decreasing the energy level caused an increase in the gross energy consumed per kilogram of gain. This trend is substantiated by Almquist et al. (1971), and by Malmberg (1972) who found that animals in the low energy group required 13 percent more gross energy per kilogram of gain than animals in the medium and high groups. Both researchers used Holstein bulls and steers as experimental animals. Gardner (1968b) and Almquist et al. (1971) pointed out that gross energy was used less efficiently for liveweight gains as their animals were fed to heavier weights. The data from these steers illustrate this trend when compared to younger animals, as shown in Table 6.

Coefficients of Apparent Digestibility

The data from the metabolism trial, reported in Tables 7 and 8, represents one animal from each treatment combination. As there is already a large volume of research done on this topic, this trial was done only to ensure that these steers exhibited digestibilities and retentions that were commensurate with the existing data. No significant differences between means were expected with so few animals,

and statistical analyses confirmed this.

TABLE 6. Comparison of the efficiency of utilization of dietary energy for liveweight gain among various weight classes of animals.

Reference	Breed	Weight Range	Energy / Gain
Gardner, 1968a	Holstein	69-110 kg.	8.72 Mcal. DE/ kg. gain
Gardner, 1968b	Holstein	91-182 kg.	13.23 Mcal. DE/ kg. gain
Malmberg, 1972	Holstein	170-300 kg.	19.10 Mcal. GE/ kg. gain
Present study	Holstein	319-413 kg.	36.03 Mcal. GE/ kg. gain

The overall average apparent digestibility coefficient for dry matter was 63.1 percent, with no differences ($P < 0.05$) due to either dietary crude protein or gross energy (Table 7). This value is lower than that of 77.0 percent reported by Kay et al. (1968) for Holstein steers of similar weight and receiving a similar diet. Malmberg (1972) also reported a higher value of 81 percent, but this was for younger animals on a primarily barley diet.

There is a suggestion from this data that the dry matter digestibility coefficients tend to decrease as the crude protein in the ration is increased. Likuski et al. (1961) reported the same trend using rats. However, Stobo et al. (1967c), Kay et al. (1968), Andrews and Ørskov (1970a) and Malmberg (1972) all reported slightly increased dry matter digestibility coefficients with increased levels of dietary crude protein. Although there were no differences or trends found in dry matter digestibility coefficients due to the level of energy fed in the present study, Gordon and Forbes (1970) and Kay et al. (1970a, 1970b, 1970c) reported a trend toward decreased dry matter digestibility coefficients in cattle when the energy level of the diet was decreased.

TABLE 7. Coefficients of apparent digestibility

Energy Level		Crude Protein Level			
		8.7%	11.9%	14.2%	
Dry Matter Digestibilities (%)					
					average
High		69.2	55.8	67.8	64.2 ^A
Medium		63.4	70.9	49.7	61.3 ^A
Low		67.3	63.0	61.3	63.9 ^A
	average	66.4 ^A	63.2 ^A	59.6 ^A	
Crude Protein Digestibilities (%)					
					average
High		62.8	48.0	67.5	59.5 ^A
Medium		46.4	66.7	52.5	55.2 ^A
Low		56.8	60.3	60.0	59.0 ^A
	average	55.3 ^A	58.3 ^A	60.0 ^A	
Gross Energy Digestibilities (%)					
					average
High		69.1	53.4	67.4	63.3 ^A
Medium		62.9	69.7	48.4	60.4 ^A
Low		67.7	62.2	61.0	63.4 ^A
	average	66.6 ^A	61.8 ^A	59.0 ^A	

^A means in the same group that are followed by a common superscript are not significantly different ($P < 0.05$).

Care must be taken in comparing results from various trials where energy levels are altered, as energy could be varied either by restriction in feed intake (Elliott et al., 1964; Andrews and Ørskov, 1970a; Robinson et al., 1970; Malmberg, 1972; and this study), or by variations in the energy concentration of the diet (Hill and Dansky, 1954; Noland and Scott, 1960; Likuski et al., 1961; Stone and Fontenot, 1965; Broster et al., 1969; Gordon and Forbes, 1970; and Kay et al., 1970b). As dry matter digestibility is generally thought to decrease with increased dry matter intake in ruminants (Maynard and Loosli, 1969), it is possible that the increased energy level may have had a beneficial effect here. ;

As pointed out by Elliott and Topps (1964), in several experiments done on protein:energy ratios, various ratios are achieved by varying the proportions of roughage to concentrate, and hence it is difficult to ascertain whether the amount of protein and/or energy, or the roughage:concentrate ratio, or both of these, affects nutrient utilization. For example, Putnam et al. (1966) found that organic matter digestibility of the ration was increased when the crude protein level for beef heifers was increased. The rations he used were high in roughage content, and had dry matter digestibilities of around 60 percent, which is considerably lower than those reported by Kay et al. (1968), using high-concentrate rations. Elliott and Topps (1964) demonstrated that with sheep, the ratio of roughage:concentrates in the diet had an effect on protein utilization, and that as the proportion of roughage is increased, increased amounts of digestible nitrogen were required for nitrogen equilibrium.

The overall average apparent digestibility coefficient for crude protein was 57.9 percent (Table 7), with no differences ($P < 0.05$) due to either dietary crude protein or gross energy. This value is lower than that of 71.6 percent reported by Kay et al. (1968) for Holstein steers of similar weight and receiving a similar diet. However, in the data reported by Kay et al. (1968), and in this study,

the digestibility of the crude protein was found to be considerably lower than the digestibility of the dry matter.

There is a possibility that the crude protein digestibility coefficients reported here may tend to follow an increasing trend as crude protein intake is increased. This trend has been reported by Pr s (1964), Putnam et al. (1966), Stobo et al. (1967a, 1967c), Kay et al. (1968), Broster et al. (1969), Gordon and Forbes (1970), Kay et al. (1970b), Lyons et al. (1970) and Malmberg (1972), all using cattle.

Although no trends are evident in this study regarding the effect of dietary gross energy on crude protein digestibility, Broster et al. (1969), Kay et al. (1970b), and Robinson et al. (1970) found that increased dietary energy resulted in increased digestibility of the crude protein, whereas Putnam et al. (1966), and Gordon and Forbes (1970) found that increased dietary energy resulted in decreased digestibility of the crude protein. As metabolic fecal nitrogen is a function of feed intake, its contribution to the fecal nitrogen increases as feed intake increases. Thus, here again, the effect of dietary energy on crude protein digestibility is dependent upon whether the dietary energy is varied by varying the feed intake, or by variation of the crude fibre content of the ration.

The overall apparent digestibility coefficient for gross energy was 62.4 percent (Table 7) with no differences ($P < 0.05$) due to either dietary crude protein or gross energy. This value is close to the value of the coefficient found for dry matter digestibility, as was expected, and is quite low compared to the value of 80 percent reported by Malmberg (1972).

The possible trend toward a decreased gross energy digestibility as the level of dietary crude protein is increased is at variance with data reported by Andrews and Ørskov (1970a), and Malmberg (1972).

No trends were evident with respect to the effect of level of dietary gross energy on gross energy digestibility in this data, but Kay et al. (1970b)

reported that energy restriction caused reduced gross energy digestibility coefficients with Holstein calves. Andrews and Ørskov (1970a), on the other hand, found lambs exhibited increased gross energy digestibility coefficients as the energy level was restricted at the lowest protein level, but otherwise there were no differences.

Urinary Crude Protein and Gross Energy Outputs and Retentions

The steers in this trial lost an overall average of 392.7 g. of crude protein per day through their urine (Table 8). Although there seems to be large differences between means, none of these were significant ($P < 0.05$) due to the small number of animals used, and the large amount of animal variation.

From this data, there is an indication that urinary crude protein excretion is increased when the protein level is increased. This trend was found by Robinson et al. (1970) and Malmberg (1972). Although the output of urinary crude protein seems to be highest at the highest energy level in this data, the opposite trend was found by Broster et al. (1969) and Robinson et al. (1970). Broster et al. (1969) reported that variation in dry matter intake did not affect urinary nitrogen excretion.

Daily crude protein retention values obtained for steers on this trial were extremely variable (Table 8) and none of the means were different ($P < 0.05$) from each other. Two of the steers lost a considerable amount of weight while on the five-day metabolism trial, which would tend to decrease nitrogen retention. It might be noted, however, that if the two negative crude protein balance values were omitted from the data, that the high protein group and the high energy group would both show superior crude protein retentions of 108.4 and 129.7 g. per day, respectively. These are results that would be expected, and are in accordance with the general principles of the effect of dietary protein and energy intake on nitrogen balance (Figure 1). Lofgreen et al. (1951), Prés (1964), Broster et al. (1969), Gordon and Forbes (1970), and Malmberg (1972) all found increases in

TABLE 8. Urinary crude protein and gross energy outputs and retentions

	Crude Protein Level			
Energy Level	8.7%	11.9%	14.2%	
Urinary Crude Protein (g./day)				average
High	481.0	365.0	738.5	528.2 ^A
Medium	183.0	434.8	339.2	319.0 ^A
Low	217.7	330.0	445.2	330.9 ^A
average	293.9 ^A	376.6 ^A	507.6 ^A	
Crude Protein Retention (g./day)				average
High	78.1 (10.2)	-169.9	181.4 (13.3)	29.8 (11.8) ^A
Medium	106.7 (17.1)	7.3 (1.1)	-51.2	20.9 (9.1) ^A
Low	97.7 (17.6)	29.1 (4.9)	35.4 (4.4)	54.1 (9.0) ^A
average	94.2 (14.9) ^A	-44.5 (3.0) ^A	55.2 (8.8) ^A	
Urinary Gross Energy (kcal/day)				average
High	883.6	632.0	1200.2	905.3 ^A
Medium	413.2	807.2	595.4	605.3 ^A
Low	506.0	590.2	722.0	606.1 ^A
average	600.9 ^A	676.5 ^A	839.2 ^A	
Gross Energy Retention (Mcal/day)				average
High	22.55 (66.5)	7.58 (49.3)	28.11 (64.7)	19.41 (60.2) ^A
Medium	16.99 (61.4)	16.68 (66.5)	7.89 (45.0)	13.85 (57.6) ^A
Low	16.15 (65.7)	13.40 (59.5)	14.88 (58.2)	14.81 (61.1) ^A
average	18.57 (64.5) ^A	12.55 (58.5) ^A	16.96 (56.0) ^A	

^A means in the same group that are followed by a common superscript are not significantly different ($P < 0.05$).

() values given in brackets represent percentages of intake.

nitrogen retention in cattle with either increases in dietary protein or energy or both. Andrews and Ørskov (1970b) and Asplund and Harris (1971) found similar trends with sheep. Sibbald et al. (1956) and Likuski et al. (1961) both reported data showing that increased digestible energy tended to increase nitrogen retention in rats.

The crude protein retention, given as a percent of the total crude protein intake for each steer, is given in brackets to the right of the daily crude protein retention values wherever the retentions were positive. The averages shown are averages of the positive retention values only. These values are fairly low, as they average around ten percent.

The steers in this trial lost an average of 705.8 kcal of energy per day through their urine (Table 8). None of the means were different ($P < 0.05$) from each other, but urinary losses of energy seemed to be highest when the dietary crude protein level was highest, and when the level of energy was highest.

The average daily gross energy retentions did not show any differences ($P < 0.05$) due to dietary crude protein or gross energy level (Table 8). The daily gross energy retention seemed to be slightly elevated however at the highest level of dietary energy. The gross energy retention, as a percent of the gross energy intake for each steer is given in brackets to the right of the daily gross energy retention values. These values indicate that about 40 percent of the gross energy that was consumed by these steers was ultimately voided through the feces and urine.

Viscera Abnormalities

At slaughter, these steers were found to have a very large number of viscera abnormalities. The parotid, submaxillary, and sublingual salivary glands in all steers were found to be normal. Three steers showed signs of tongue erosion, and one steer was diagnosed as having actinomycosis. Two steers had heart adhesions, and one had inflamed heart muscles. All of these steers with the tongue and heart

abnormalities were in the group fed the low and medium levels of protein. All three steers with abnormal hearts were receiving the high level of energy.

There were six steers that had inflammation, congestion, or adhesions of the lungs. These steers were found in almost all treatment combinations, and it is quite likely that these conditions may have existed before the steers started the trial.

Two steers on the high energy level of feeding, and one steer on the medium energy level of feeding had abscessed rumens. Two steers on the high protein - low energy treatment had adhesions of the rumen and intestines.

Eleven of the twenty-seven steers slaughtered had abnormalities of one or both kidneys. These kidney abnormalities were fairly randomly spread as far as dietary crude protein levels were concerned, with low, medium, and high protein groups having four, three, and four steers with bad kidneys, respectively. The high, medium, and low energy groups had five, four, and two animals with bad kidneys, respectively, which possibly might indicate a trend to more kidney problems at the higher levels of feeding. It is most likely, however, that these conditions existed prior to purchase of these steers.

Seventeen, or approximately 63 percent of these steers, had liver abnormalities, with most of these classified as liver abscesses. The low, medium, and high protein groups contained four, five, and eight steers respectively with liver abnormalities. The high, medium, and low energy groups contained eight, five, and four steers, respectively, with liver abnormalities. The trend seems to be directed toward a higher incidence of liver abscesses or other abnormalities with either an increase in dietary crude protein content, or an increase in dietary gross energy. However, as mentioned before, many of these abnormal viscera conditions could have been present when the steers were purchased. As these steers came out of a commercial feedlot, there is no record of prior treatment, but it is

likely that they were subject to a rigorous feeding program.

The incidence of liver damage seems high in this trial. Rowland (1970), and Foster and Woods (1971) reported percentages of abscessed livers in market cattle of 25 and 33 percent in 2500 head and 220 head, respectively. Both these groups also found that the incidence of liver abscesses was higher on an all-concentrate ration than on a ration containing some roughage. However, Grieve (1966, 1968) and Malmberg (1972) both used high-grain rations for fattening Holsteins, and reported very few abnormal livers. Foster and Woods (1971) reported that animals with liver abscesses had daily gains depressed by about six percent compared to animals with normal livers. This factor, as well as the multitude of other viscera abnormalities may well account for the low daily gains obtained by steers in this trial.

Kidney Fat, Backfat Thickness, and Marbling

The average values obtained for weight of kidney fat from the left side of the carcass, the fat thickness over the longissimus dorsi muscle between the 11th and 12th ribs, and the marbling score, are shown in Table 9. The weight recorded for kidney fat represents the combined weight of fat around the left kidney and pelvic fat from the left side of the carcass. The backfat thickness recorded is the average of three measurements taken by a Canada Department of Agriculture government grader.

The effects of increasing dietary crude protein and gross energy on the amount of kidney fat deposited by these steers were not significant ($P < 0.05$) but there is a suggestion that internal fat deposition may have been depressed at the medium protein level, and enhanced at the medium energy level (Table 9). There is no logical explanation for such a trend, but it may be noted that Malmberg (1972) also found the weight of kidney fat was depressed somewhat at the medium

TABLE 9. Kidney fat, backfat thickness, and marbling

Energy Level	Crude Protein Level			
	8.7%	11.9%	14.2%	
Average Weight of Kidney Fat (kg.)				
				average
High	2.7	1.9	2.7	2.3 ^A
Medium	2.7	2.5	3.0	2.8 ^A
Low	2.3	1.8	2.3	2.2 ^A
	average	2.6 ^A	2.1 ^A	2.5 ^A
Average Fat Thickness Over <u>L. Dorsi.</u> (cm.)				
				average
High	.74	.39	.59	.57 ^A
Medium	.98	.62	.69	.76 ^A
Low	.67	.54	.82	.68 ^A
	average	.80 ^A	.52 ^A	.70 ^A
Marbling Score *				
				average
High	8.0	8.0	8.7	8.2 ^b
Medium	7.3	7.3	7.7	7.4 ^a
Low	7.0	7.3	7.0	7.1 ^a
	average	7.4 ^A	7.6 ^A	7.8 ^A

a, b

means in the same group that are followed by a common superscript are not significantly different ($P < 0.01$).

A

means in the same group that are followed by a common superscript are not significantly different ($P < 0.05$).

*

Marbling Score: increased numerical value from 1 to 10 denotes decreased marbling.

protein level. Kliewer et al. (1970) reported estimated kidney fat percent to drop from 2.8 to 2.4 percent when the crude protein level of the ration for Holstein steers was raised from 11 to 15 percent. The use of weight of kidney fat as an estimate of carcass yield has been used by several authors. Kirchner et al. (1968) and Richardson et al. (1968) both used kidney fat along with other independent variables in attempts to develop prediction equations for carcass yields.

The effects of dietary crude protein and gross energy on the average fat thickness over the longissimus dorsi, between the 11th and 12th ribs were not significant ($P < 0.05$), but again there is a suggestion that fat cover may have been depressed at the medium protein level, and enhanced at the medium energy level (Table 9). These values may not be too meaningful however, as the 100 kg. of liveweight gained by these steers was probably insufficient to test differences in fat cover.

Kliewer et al. (1970) found an interaction between fat thickness response to diethylstilbestrol (DES) and protein level with Holstein steers. At high protein levels, implanting with DES suppressed fat thickness, but at low protein levels, implanting with DES increased fat thickness. They also found that in general, as the dietary crude protein level was raised, the thickness of backfat increased. Likuski et al. (1961) found that increasing the dietary energy level of pigs increased the average backfat, but that increasing the dietary protein level decreased the average backfat. An interaction resulted, as increasing the protein level of low energy rations decreased backfat more than increasing the protein level of the high energy rations. Epley et al. (1970b) reported that fat trim was not affected by varying the protein to energy ratio in rations for Hereford steers.

Fat thickness has often been used in an attempt to evaluate the degree of fatness of an animal. Fitzhugh et al. (1965), Hedrick et al. (1965), Busch et al. (1968), Epley et al. (1970a), and Moody et al. (1970) all reported significant

correlations of fat thickness with either weight or percent of retail cuts from steer carcasses. Wellington (1970) reported fat thickness to be significantly correlated with grade in dairy beef.

The marbling scores assigned to the carcasses of these steers (Table 9) were not affected by the dietary crude protein level ($P < 0.05$), but were affected by the gross energy level ($P < 0.01$). The marbling scores for the high, medium, and low energy groups were 8.2, 7.4, and 7.1, respectively. The high energy group had a marbling score that was approximately 13 percent higher ($P < 0.01$) than that obtained by steers fed the other two energy levels. Thus, at the high energy level, less fat was deposited in the lean tissues at all dietary protein levels. Wellington (1970) reported a significant ($P < 0.05$) correlation between marbling score and days on test, which was essentially equal to days of age, for 137 Holstein steers. The trend of his data was to increased marbling with a longer feeding period. Reference to Table 4 shows that the results of this trial are in agreement, as those animals with the least amount of marbling were in fact on feed for the shortest period of time.

Kliwer et al. (1970) found at high protein levels, implanting with DES depressed the amount of marbling, but at low protein levels, implanting with DES increased the amount of marbling in the carcass. This is an interaction similar to that found with backfat thickness by the same author. Moody et al. (1970) found in Angus steers that marbling score was highly correlated with the percent of the edible portion of the carcass.

Dressing Percentage, Rib-Eye Area, Cutability, and Grade

Average values obtained for dressing percentage, rib-eye area, and cutability of the steers are shown in Table 10. The dressing percentage was calculated as warm dressed weight of the carcass divided by the liveweight of the steer the morning of its slaughter. The rib-eye area is the cross-sectional area (square centi-

TABLE 10. Dressing percentage, rib-eye area, and cutability

Energy Level	Crude Protein Level			
	8.7%	11.9%	14.2%	
	Dressing Percentage (%)			average
High	55.7	56.1	53.6	55.1 ^A
Medium	54.5	57.3	58.2	56.6 ^A
Low	58.0	54.8	56.1	56.3 ^A
	average	56.0 ^A	56.1 ^A	56.0 ^A
	Rib-Eye Area per 100 kg. Liveweight (cm. ²)			average
High	12.6	13.0	13.0	12.9 ^A
Medium	13.6	14.9	12.8	13.8 ^A
Low	14.9	13.2	13.8	14.0 ^A
	average	13.7 ^A	13.7 ^A	13.2 ^A
	Cutability (%)			average
High	47.9	48.6	47.9	48.2 ^A
Medium	47.1	47.3	48.1	47.5 ^A
Low	47.2	48.1	47.2	47.5 ^A
	average	47.4 ^A	48.0 ^A	47.8 ^A

^A means in the same group that are followed by a common superscript are not significantly different ($P < 0.05$).

meters) of the longissimus dorsi between the 11th and 12th rib as determined by Canada Department of Agriculture grading standards. These values are expressed per 100 kg. of liveweight to reduce possible variations due to size of the animal. The cutability values for these steers were calculated from the United States Department of Agriculture Yield Grade Cutability Equation developed by Murphey et al. (1960). This equation yields cutability in terms of percent of boneless retail cuts from the round, loin, rib, and chuck. The equation is:

$$\begin{aligned} \text{Cutability} = & 51.34 - 2.276 (\text{fat thickness over rib-eye, cm.}) \\ & - 0.0205 (\text{hot carcass weight, kg.}) - 0.462 (\text{kidney fat, \%} \\ & \text{of carcass}) + 0.115 (\text{area of rib-eye, sq. cm.}). \end{aligned}$$

The overall average dressing percentage of all 27 steers was 56.0 percent. There were no differences ($P < 0.05$) due to crude protein or gross energy levels. Robertson et al. (1970) could not detect any differences in dressing percentages of beef carcasses with changes in the level of crude protein. Although Malmberg (1972) found the dressing percentage of male Holstein carcasses was depressed ($P < 0.05$) when the animals were on a low protein diet, he found no differences ($P < 0.05$) due to dietary energy level. Kliewer et al. (1970) noted a slight decrease in carcass yield when the crude protein level for Holstein steers was raised from 11 to 15 percent. Likuski et al. (1961) found that increased energy intakes led to increased dressing percentages in swine carcasses. Due to the inconsistencies reported in the literature, it is difficult to come to any conclusions regarding the effect of dietary protein and energy on dressing percentage.

No differences ($P < 0.05$) were found in average values for rib-eye area per unit weight for these steers (Table 10). The actual rib-eye areas (unadjusted for weight) did not show any differences ($P < 0.05$) either (Appendix B). The steers receiving the high protein ration were slightly heavier than steers in the other two protein groups (Table 4), but yet these steers had a slightly smaller rib-

eye area per 100 kg. of liveweight than steers in the other two protein groups (Table 10). This illustrates a point made by Hedrick et al. (1965), and Moody et al. (1970) that rib-eye area increased as cattle became older and larger, but that the increase was not proportional. Thus, on a unit weight basis, rib-eye area decreased as weight increased. A similar trend was not evident for rib-eye areas with respect to the level of energy fed. Malmberg (1972) found that rib-eye area was affected ($P < 0.01$) by the level of protein in the diet, but concluded that these differences were probably indicative of variations in carcass weight.

The measurement of rib-eye area has been used extensively in attempts to make various quantitative and qualitative estimates of lean meat, or edible meat yield from a carcass. Fitzhugh et al. (1965), Busch et al. (1968), Kirchner et al. (1968), Richardson et al. (1968), and Moody et al. (1970) all found good correlations of rib-eye area with edible meat from beef carcasses. Hedrick et al. (1965), and Epley et al. (1970a) both stressed that rib-eye area was more highly correlated with weight, rather than percent of retail cuts obtained from a carcass. However, Fitzhugh et al. (1965), Busch et al. (1968), Nelms et al. (1968), and Epley et al. (1970a) all pointed out that rib-eye area by itself is not a very good estimator of retail meat yield without the inclusion of carcass weight in a prediction equation.

There was very little variation in the cutability values obtained from the steers in this trial (Table 10). The overall average cutability was 47.7 percent, and there were no differences ($P < 0.05$) due to the dietary crude protein or gross energy levels. This value is only slightly lower than the cutability values reported by Berg (1969) for Brown Swiss steers, and Ziegler et al. (1971) for Holstein steers, of 48.6 and 49.4 percent, respectively.

Ziegler et al. (1971) noted that animals with the highest cutabilities were not readily acceptable as beef because of less tenderness and juiciness than animals with the lowest cutabilities. These workers found cutability was significantly and

positively correlated (slaughter age and weight held constant) with marbling ($P < 0.05$) and flavor ($P < 0.01$), and significantly and negatively correlated with tenderness, juiciness, and total acceptability. There seems to be no indication in the data from the present study that cutability and marbling are correlated. Powell and Huffman (1968) compared various quantitative estimates of beef carcass composition and concluded that, considering prediction accuracy and practical aspects of each method, the yield grade equation (Murphey et al., 1960) was the best evaluation method.

Almost all of the carcasses graded were lacking fleshing and finish. The grades ranged from Canada Manufacturing to Canada Good. Most of the steers graded Canada Standard. The steers receiving the low protein ration had the best grades. In this group, six graded Canada Standard, and three graded Canada Commercial (class 1). In the medium and high protein groups, more carcasses graded Canada Commercial (class 1) or lower, than graded Canada Standard or higher. The steers receiving the medium energy level had better grades than the steers in the other two energy groups. Six of the steers graded Canada Standard, and three of the steers graded Canada Commercial (class 1) in the medium energy group. Again, in the other groups, more carcasses graded Canada Commercial (class 1) or lower, than graded Canada Standard or higher.

Physical Analysis of Rib Samples

Differences among the steers in the percent of separable lean, fat, and bone of the tenth rib section (Table 11) were small and nonsignificant ($P < 0.05$). The maximum percent of separable lean was obtained from steers which were fed the medium level of protein. Increasing the dietary energy at the low protein level seemed to decrease the percentage of separable lean, but seemed to slightly increase the percentage of separable lean at the high protein level. The percentage

TABLE 11. Separable lean, fat, and bone of the tenth rib

Energy Level		Crude Protein Level			
		8.7%	11.9%	14.2%	
Average Separable Lean (%)					
					average
High		59.3	65.4	61.6	62.1 ^A
Medium		61.3	61.4	61.5	61.4 ^A
Low		62.0	62.7	61.2	62.0 ^A
	average	60.8 ^A	63.2 ^A	61.4 ^A	
Average Separable Fat (%)					
					average
High		25.4	19.9	22.7	22.7 ^A
Medium		24.7	22.7	22.3	23.2 ^A
Low		21.2	19.8	22.9	21.3 ^A
	average	23.8 ^A	20.8 ^A	22.6 ^A	
Average Separable Bone (%)					
					average
High		15.3	14.7	15.7	15.2 ^A
Medium		14.0	15.8	16.2	15.3 ^A
Low		16.9	17.4	15.9	16.7 ^A
	average	15.4 ^A	16.0 ^A	15.9 ^A	

^A means in the same group that are followed by a common superscript are not significantly different ($P < 0.05$).

separable lean was slightly lower for steers fed the medium energy level than for steers fed the other two energy levels.

The average values obtained from the data for percent separable fat of the tenth rib show a tendency toward minimum fat at the medium protein level, and maximum fat at the medium energy level (Table 11), although these differences were not significant ($P < 0.05$). This trend has been noted before, both in the average weight of kidney fat, and in the average fat thickness over the longissimus dorsi (Table 9). The average percent separable fat seems to respond positively to increases in dietary energy only at the low protein level. This may be because at this low level of dietary protein, very little energy is required to metabolize it, and hence increases in dietary energy may be channeled into body fat. As more and more dietary crude protein is supplied, the increases in dietary energy become less and less effective in causing body fat deposition. This is illustrated by the fact that the maximum values for percent separable fat occur on a diagonal line through the data, with maximum separable fat at the high energy level for low protein, the medium energy level for medium protein, and the low energy level for high protein.

Average separable bone from the tenth rib of these steers is reported only because it was the third component of the total rib. None of the means are different ($P < 0.05$), and the percent bone in the low energy group of steers is slightly higher than the others due to chance only.

Several authors, using various species of experimental animals, have shown increased fat in the carcass due to increased dietary energy (Hill and Dansky, 1954; Noland and Scott, 1960; Wagle et al., 1962; Elsley et al., 1964; Almquist et al., 1971; and Waldman et al., 1971). Such data is in agreement with Blaxter's (1966) concept that despite a wide range in growth rate, the amount of edible protein produced from a given amount of feed varies very little, but the amount of edible fat varies considerably.

Both Andrews and Ørskov (1970b) and Norton et al. (1970) reported that increased dietary protein resulted in decreased fat deposition, and increased protein deposition in lamb carcasses. Andrews and Ørskov (1970b) found this effect particularly marked at the high level of feeding, which tends to agree with the statement made earlier that less body fat may be deposited as more and more of the dietary energy is used in metabolizing protein.

The use of the 9-10-11 rib cut and prediction equations as a "shortcut" was popularized by the work of Hankins and Howe (1946), and there are several recent reports which employ these same principles (Almquist et al., 1971; Field, 1971; Moody et al., 1970; Waldman et al., 1971; and Warwick et al., 1971). Several authors have used the tenth rib only (Preston et al., 1963a, 1963b; Kay et al., 1967, 1968, 1970d; Malmberg, 1972) as was done in this study.

Chemical Analyses of Rib Samples

Chemical analyses of the separable lean and fat from the rib samples is shown in Table 12. There were no differences ($P < 0.05$) in the average crude protein content of the separable lean of the tenth rib due to either dietary crude protein level or dietary gross energy level fed. The overall average value was 74.4 percent crude protein in the lean on a dry-matter basis, which is slightly lower than the value of 80 percent reported for younger Holstein bulls and steers by Malmberg (1972). There seemed to be a tendency for the percent crude protein in the lean to decrease at the high protein level. Perhaps this is a sign that the protein level was too high, inasmuch as protein was wasted at this level, and was not incorporated into the lean body tissues. The percent crude protein of the lean seems to show a minimum at the medium energy level which fits in with the maximum in percent ether extract of the lean which is exhibited at that level.

There were no differences ($P < 0.05$) in the average ether extract content

TABLE 12. Chemical analysis of the tenth rib

Energy Level	Crude Protein Level			
	8.7%	11.9%	14.2%	
Average Crude Protein of the Lean (% of D.M.)				
				average
High	75.8	77.2	73.7	75.6 ^A
Medium	73.4	74.2	71.7	73.1 ^A
Low	75.7	73.9	73.8	74.5 ^A
	average	75.0 ^A	75.1 ^A	73.1 ^A
Average Ether Extract of the Lean (% of D.M.)				
				average
High	19.0	16.5	22.9	19.5 ^A
Medium	21.4	21.6	23.6	22.2 ^A
Low	21.4	20.9	23.1	21.8 ^A
	average	20.6 ^A	19.6 ^A	23.2 ^A
Average Dry Matter of the Fat (% — Freeze-dried)				
				average
High	84.7	81.1	80.7	82.1 ^A
Medium	85.9	79.7	84.1	83.2 ^A
Low	82.2	76.9	83.2	80.8 ^A
	average	84.2 ^A	79.2 ^B	82.7 ^{AB}
Average Crude Protein of the Fat (% of Freeze-dried)				
				average
High	6.3	9.4	6.3	7.4 ^I
Medium	5.8	6.6	6.0	6.1 ^I
Low	6.9	8.0	7.0	7.3 ^I
	average	6.3 ^I	8.0 ^{II}	6.4 ^I

A, B means in the same group that are followed by a common superscript are not significantly different ($P < 0.05$).
I, II means in the same group that are followed by a common superscript are not significantly different ($P < 0.10$).

of the separable lean of the tenth rib due to either dietary crude protein or gross energy levels (Table 12). The data tend to show minimum fat in the lean at the medium protein level, and maximum fat in the lean at the medium energy level. This is in keeping with the trends shown by kidney fat weight and backfat thickness (Table 9) and percent separable fat in the tenth rib (Table 11). It may be noted that the steers in this trial showed an overall average ether extract in the separable lean of the tenth rib of 21.2 percent, which is considerably higher than the 15.8 percent value reported by Malmberg (1972), thus indicating that these animals had considerably more marbling than the younger animals. The data obtained in this study for percent ether extract of the separable lean in the tenth rib seem to correlate somewhat with the reported marbling scores (Table 9). For example, within each dietary crude protein level, both the marbling scores and the values for percent ether extract in the lean indicate the least amount of marbling at the high energy level.

The average dry matter content of the separable fat from the tenth rib of these steers was affected ($P < 0.10$) by the dietary crude protein level, but not by the dietary energy level (Table 12). The average percent dry matter for the separable rib fat for steers receiving the low, medium, and high protein levels was 84.2, 79.2, and 82.7 percent, respectively. The steers receiving the medium and high protein levels had less ($P < 0.05$) dry matter in the separable rib fat than those on the low protein level, and steers receiving the low and high protein levels had more ($P < 0.05$) dry matter in the separable rib fat than those on the medium protein level.

The average percent crude protein of the separable fat of the tenth rib of these steers was also affected ($P < 0.10$) by the dietary crude protein level, but not by the dietary energy level (Table 12). The average percent crude protein of the separable rib fat for steers receiving the low, medium, and high protein levels

was 6.3, 8.0, and 6.4 percent, respectively. The steers receiving the medium level of protein had more ($P < 0.10$) crude protein in the separable rib fat than steers receiving the low or high protein levels. This maximum value may be coincident with some of the physical data reported. That is, at the medium protein level, steers tended to put on a greater proportion of lean meat, and a lower proportion of fat, and the fat was quite high in crude protein.

The average percent dry matter content of the separable lean from the tenth rib of these steers showed extremely little variation, and was not reported. The average percent dry matter values for the separable rib lean from steers receiving the low, medium, and high protein rations was 27.7, 26.9, and 27.4, respectively. The average percent dry matter values for the separable rib lean from steers receiving the high, medium, and low energy levels was 27.2, 27.3, and 27.4, respectively. None of the differences between means were significant ($P < 0.05$).

Other authors that have reported on chemical analysis of the tenth rib have done the analysis on the entire rib section, without physical separation, and hence comparisons are difficult to make. Preston et al. (1963a) reported that in the entire tenth rib cut from Holstein steers slaughtered at 400 kg. liveweight, ether extract was 22.5 percent, protein was 17.5 percent, ash was 4.64 percent, and moisture was 54.4 percent. In another study on Holstein steers slaughtered at 405 kg. liveweight, (Preston et al. 1963b) the tenth rib cut was found to contain 24.0 percent ether extract, 17.1 percent protein, 5.0 percent ash, and 53.3 percent moisture. Using the reported values for the physical and chemical data on separable lean and fat in this trial, the overall average ether extract, crude protein, and moisture content of the complete tenth rib cut was 17.4, 13.8, and 49.0 percent, respectively. These figures are all somewhat lower than those reported by Preston et al. (1963a, 1963b) and are open to considerable error due

to their means of calculation.

Kay et al. (1967, 1968) using Holstein steers slaughtered at 400 kg. and 350 kg. liveweight found that chemical analyses of the tenth rib joint showed no significant differences ($P < 0.05$), but there was a suggestion that the fat content was higher and the water content lower in the ribs from the steers given the high protein diet compared with those receiving the low protein diet. There was no such trend in the data from this trial, however.

A comparison of the physical and chemical data from the tenth ribs of the steers in this study, and of the animals in a study done by Malmberg (1972) demonstrates age and weight differences between carcasses from the same breed (Table 13).

TABLE 13. Comparison of Carcass Characteristics of Two Weight-Groups of Holstein Males

Weight Range of Holstein Males Studied	Tenth Rib Analyses					
	% Sep. Lean	% Sep. Fat	% C.P. of Lean	% E.E. of Lean	% D.M. of Fat	% C.P. of Fat
170-300 kg. (Malmberg, 1972)	64.6	18.3	80.0	15.8	69.3	15.6
319-413 kg. (Present study)	61.8	22.4	72.7	21.2	82.0	6.9

It can be seen that as the animals become older and heavier, their carcasses contain a lower percentage of lean meat, and a higher percentage of fat. Also, the lean meat contains less protein, but more fat due to increased marbling. The fat seems to lose moisture with increased animal weight, and contains less crude protein. These trends demonstrate what is currently known about the aging and fattening process of animals.

SUMMARY

Steers fed the high energy level had the highest average daily gains, followed by steers fed the medium and low energy levels. Daily gain was not significantly affected by dietary crude protein level, but gains were highest and almost identical at the medium protein-high energy level, and the high protein-high energy level. The protein:energy ratio at the medium protein-high energy level was 32.0 g. of crude protein per Mcal of gross energy, which appeared to be the optimum ratio. There appeared to be a trend toward a decreased benefit to adding extra energy beyond the medium energy level when the protein was at the low level. There also appeared to be a decreased benefit to adding extra protein beyond 11.9 percent when energy was at the low level.

Multiple regression analyses were done on the data to develop prediction equations which would describe response surfaces. However, as the data were limited, response surface methodology was used more to illustrate its potential as a biological research tool, than to arrive at a precise mathematical description of the form of the data.

The efficiency of utilization of dry matter and gross energy for liveweight gain tended to increase with increasing crude protein, and decrease with decreasing gross energy. The efficiency of utilization of crude protein for liveweight gain decreased with increasing crude protein, and with decreasing gross energy.

The coefficients of apparent digestibility of dry matter, crude protein, and gross energy were lower than expected, probably due to the large number of viscera abnormalities in these steers. The apparent digestibility coefficients for dry matter and gross energy indicated that the digestibility decreased as the crude protein level increased, with a suggestion that the trend was reversed for crude protein digestibility.

Daily crude protein retentions were variable and quite low. Daily gross energy retentions were also quite variable. Losses of crude protein and gross energy

through the urine seemed to be highest from the steers when the dietary crude protein level was increased, and when the high energy level was fed.

The percentages of separable lean and fat from the tenth rib of these steers suggested that the steers receiving the medium protein level had a higher percentage of lean, and a lower percentage of fat in their carcasses than the steers fed the other crude protein levels. There was a similar suggestion that the steers receiving the medium energy level had a higher percentage of fat, and a lower percentage of lean in their carcasses than the steers fed the other gross energy levels. The medium protein-high energy group exhibited the highest percentage of separable lean relative to separable fat from the tenth rib.

The weight of kidney fat, and the backfat thickness both were lowest in the steers fed the medium protein level, and highest in the steers fed the medium energy level. The least amount of marbling in the steer carcasses was recorded at the high energy level. Steers receiving the high protein and high energy levels had the smallest rib-eye area per unit weight, but this may have been affected by the fact that these steers were slightly heavier than the average. Steers receiving the low protein level, and steers receiving the medium energy level graded higher than steers in the other groups.

Chemical analyses of the separable rib lean and fat indicated that the separable rib lean from steers receiving the medium protein level contained a lower percentage of fat than that from steers fed the other crude protein levels. Also, the separable rib lean from steers receiving the medium energy level contained a higher percentage of fat than that from steers fed the other gross energy levels. Steers fed the high energy level had the lowest percentage of fat in the separable rib lean, which, like the amount of marbling, may have been due to the fact that this group was on feed for the shortest length of time. The percentage of dry matter in the separable rib fat was lowest for steers receiving the medium protein level.

The percentage of crude protein in the separable rib fat was highest for steers receiving the medium protein level, and lowest for steers receiving the medium energy level.

The overall optimum combination of dietary crude protein and gross energy for the steers in this trial appeared to be the medium protein-high energy level, that is, an 11.9 percent crude protein diet fed ad libitum. This treatment combination appeared to produce best liveweight gains with relatively good efficiency. Also, the steers consuming the medium protein level tended to put on a higher proportion of lean meat and a lower proportion of fat, with the fat being quite high in crude protein. Indications were that steers receiving the high level of energy had the least intramuscular fat.

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APPENDIX

Appendix Table A.

The derivation of isoquants

(OECD, 1966)

The derivation of isoquants from an equation of the form

$$Y = a + b_1X_1 + b_2X_2 + b_3X_1^2 + b_4X_2^2 + b_5X_1X_2$$

is as follows:

(1) rearrange the equation thus

$$b_3X_1^2 + (b_1 + b_5X_2)X_1 + (a + b_2X_2 + b_4X_2^2 - Y) = 0$$

which is a quadratic equation in X_1

(2) apply the general formula for solution of a quadratic equation to produce the isoquant equation,

$$X_1 = \frac{-(b_1 + b_5X_2) \pm \sqrt{(b_1 + b_5X_2)^2 - 4b_3(a + b_2X_2 + b_4X_2^2 - Y)}}{2b_3}$$

which may be solved for X_1 given various levels of Y and X_2 .

Appendix Table B. Mean squares obtained by analysis of variance.

Variable	Source of Variation	Degrees of Freedom	Mean Squares
CP/day	Protein	2	351011.8**
	Energy	2	75779.4**
	PXE	4	3421.3
	Error	17	10689.1
	Total	25	
GE/day	Protein	2	1.278
	Energy	2	79.741**
	PXE	4	2.929
	Error	17	8.864
	Total	25	
Gain/day	Protein	2	.0173
	Energy	2	.2065**
	PXE	4	.0036
	Error	17	.0259
	Total	25	
Initial Weights	Protein	2	87.6
	Energy	2	122.3
	PXE	4	258.5
	Error	17	732.9
	Total	25	
Final Weights	Protein	2	630.62
	Energy	2	1059.37
	PXE	4	455.20
	Error	17	1113.86
	Total	25	
Days on Feed	Protein	2	339.15
	Energy	2	1651.37**
	PXE	4	52.93
	Error	17	168.35
	Total	25	
DM/day	Protein	2	.1195
	Energy	2	4.2462**
	PXE	4	.1541
	Error	17	.4698
	Total	25	

Variable	Source of Variation	Degrees of Freedom	Mean Squares
DM/gain	Protein	2	2.140
	Energy	2	3.989
	PXE	4	1.686
	Error	17	1.565
	Total	25	
CP/gain	Protein	2	.3738**
	Energy	2	.0661°
	PXE	4	.0212
	Error	17	.0222
	Total	25	
GE/gain	Protein	2	43.012
	Energy	2	75.003
	PXE	4	31.703
	Error	17	29.465
	Total	25	
Coefficient of Dry Matter Digestibility	Protein	2	37.080
	Energy	2	7.526
	PXE	4	71.249
	Total	8	
Coefficient of Crude Protein Digestibility	Protein	2	16.896
	Energy	2	16.626
	PXE	4	99.785
	Total	8	
Coefficient of Gross Energy Digestibility	Protein	2	44.387
	Energy	2	9.874
	PXE	4	80.391
	Total	8	
Urine C.P.	Protein	2	1080747.1
	Energy	2	787317.7
	PXE	4	351474.6
	Total	8	
C.P. retained/day	Protein	2	15348.55
	Energy	2	880.66
	PXE	4	12532.78
	Total	8	

Variable	Source of Variation	Degrees of Freedom	Mean Squares
% C.P. retained	Protein	2	544.41
	Energy	2	172.55
	PXE	4	323.92
	Total	8	
Urine G.E.	Protein	2	1.112
	Energy	2	2.244
	PXE	4	1.092
	Total	8	
GE retained/day	Protein	2	29.071
	Energy	2	26.516
	PXE	4	56.150
	Total	8	
% G.E. retained	Protein	2	58.023
	Energy	2	9.733
	PXE	4	86.361
	Total	8	
Weight of kidney fat	Protein	2	.6544
	Energy	2	.8933
	PXE	4	.0994
	Error	17	.6510
	Total	25	
Backfat Thickness	Protein	2	.1814
	Energy	2	.0807
	PXE	4	.0405
	Error	17	.0727
	Total	25	
Marbling Score	Protein	2	.2593
	Energy	2	2.9259**
	PXE	4	.2037
	Error	17	.3137
	Total	25	
Dressing Percentage	Protein	2	.0155
	Energy	2	5.8096
	PXE	4	12.3306
	Error	17	6.2267
	Total	25	

Variable	Source of Variation	Degrees of Freedom	Mean Squares
Rib-Eye Area (REA)	Protein	2	5.0646
	Energy	2	38.6008
	PXE	4	40.2071
	Error	17	65.6412
	Total	25	
REA/100 kg. weight	Protein	2	.7494
	Energy	2	3.1123
	PXE	4	2.4791
	Error	17	2.1724
	Total	25	
Cutability	Protein	2	.8106
	Energy	2	1.3015
	PXE	4	.6715
	Error	17	.9078
	Total	25	
% Lean in Tenth Rib	Protein	2	13.3878
	Energy	2	1.1633
	PXE	4	8.4444
	Error	17	13.3404
	Total	25	
% Fat in Tenth Rib	Protein	2	19.6933
	Energy	2	9.0844
	PXE	4	7.4078
	Error	17	14.8372
	Total	25	
% Bone in Tenth Rib	Protein	2	.9740
	Energy	2	6.3737
	PXE	4	2.8993
	Error	17	4.2149
	Total	25	
% C.P. in lean	Protein	2	11.7893
	Energy	2	13.6004
	PXE	4	2.9159
	Error	17	13.9592
	Total	25	

Variable	Source of Variation	Degrees of Freedom	Mean Squares
% E.E. in lean	Protein	2	30.5159
	Energy	2	19.6359
	PXE	4	4.5404
	Error	17	13.9718
	Total	25	
% DM in fat	Protein	2	59.7737°
	Energy	2	13.5070
	PXE	4	9.9865
	Error	17	18.5541
	Total	25	
% C.P. in fat	Protein	2	7.8048°
	Energy	2	4.2504
	PXE	4	1.7570
	Error	17	2.8208
	Total	25	
% DM in lean	Protein	2	1.3082
	Energy	2	.0404
	PXE	4	.4459
	Error	17	1.0400
	Total	25	

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